Ants Bees and Wasps

PLATE I

Fig. 1. *Lasius niger*, worker (× 6)

,, 2. *Myrmica ruginodis*, worker (× 6)

,, 3. *Formica fusca*, worker (× 5)

,, 4. *Lasius flavus*, worker (× 6)

,, 5. *Polyergus rufescens*, worker. The Amazon ant (× 5)

,, 6. *Formica sanguinea*, worker. The blood-red slave-maker (× 5)

[*Front*

Ants Bees and Wasps

A Record of Observations on the Habits of the Social Hymenoptera

By
SIR JOHN LUBBOCK
(LORD AVEBURY)
F.R.S., D.C.L., etc.

New Edition, Based on Seventeenth,
Edited and Annotated by
J. G. MYERS
SC.D., F.E.S.

WITH 4 COLOURED PLATES BY
A. J. E. TERZI

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AUTHOR'S PREFACE

This volume contains the record of various experiments made with ants, bees, and wasps during the past ten years; and most of which have appeared in the *Journal of the Linnean Society* for the years 1874 to 1882. Other occupations and many interruptions, political and professional, have prevented me from making them so full and complete as I had hoped. My parliamentary duties, in particular, have absorbed most of my time just at the season of year when these insects can be most profitably studied. I have, therefore, whenever it seemed necessary, carefully recorded the month during which the observations were made; for the instincts and behaviour of ants, bees, and wasps are by no means the same throughout the year. My object has been not so much to describe the usual habits of these insects as to test their mental condition and powers of sense.

Although the observations of Huber, Forel, McCook and others are no doubt perfectly trustworthy, there are a number of scattered stories about ants which are quite unworthy of credence; and there is also a large class in which, although the facts may be correctly recorded, the inferences drawn from them are very questionable. I have endeavoured, therefore, by actual experiments which any one may, and I hope others will, repeat and verify, to throw some light on these interesting questions.

The principal point in which my mode of experimenting has differed from that of previous observers has been that I have carefully marked and watched particular insects; and secondly, that I have had nests under observation for long periods. No one before had ever kept an ants' nest for more than a few months. I have one now in my room which has been under constant observation ever since 1874, i.e. for more than seven years.*

* I may add that these ants are still (August, 1882) alive and well. The queens at least are now eight years old, if not more. [These lived much longer. See Chaps. I and II.—Ed. Note.]

I had intended to make my observations principally on bees; but I soon found that ants were more convenient for most experimental purposes, and I think they have also more power and flexibility of mind. They are certainly far calmer, and less excitable.

I do not attempt to give anything like a full life-history of ants, but I have here reproduced the substance of two Royal Institution lectures, which may serve as an introduction to the subject. Many of the facts there recorded will doubtless be familiar to most of my readers, but without the knowledge of them the experiments described in the subsequent chapters would scarcely be intelligible.

I have given a few plates illustrating some of the species to which reference has been most frequently made; selecting Lithography (as I was anxious that the figures should be coloured), and having all the species of ants drawn to one scale, although I was obliged in some measure to sacrifice the sharpness of outline, and the more minute details.* I am indebted to Mr Bates, Dr Günther, Mr Kirby, and Mr Waterhouse for their kind assistance in the preparation of the plates.

As regards bees and wasps, I have confined myself for want of space to the simple record of my own observations.

I am fully conscious that experiments conducted as mine have been leave much to be desired, and are scarcely fair upon the ants. In their native haunts and under natural conditions, more especially in warmer climates, they may well be expected not only to manifest a more vivid life, but to develop higher powers.

I hope, however, that my volume will at least show the great interest of the subject, and the numerous problems which still remain to be solved.

HIGH ELMS, DOWN, KENT.
18th October, 1881.

* [These plates are not reproduced in the present edition. The coloured plates especially prepared for this edition are designed to show as much detail as space will allow, and to indicate the size of the insects by lines beside every figure.—ED. NOTE.]

EDITOR'S FOREWORD

THE popularity of Lubbock's classical work on the ants, bees, and wasps is sufficiently attested by the fact that since 1882 no fewer than seventeen editions have been issued.

During this period the social insects, and above all, the ants, have continued to attract to their study investigators of the highest order. We now know much more about these insects and their marvellous social organization than Lubbock knew. It was therefore thought useful, in the present edition, while leaving Lubbock's orginal text unaltered, to supply at the end of the book a series of notes on the more important points which have been elucidated in recent years, or on which Lubbock's results have been either corroborated or refuted. These notes are cited at the appropriate places by means of small consecutive numbers, while Lubbock's own foot-notes are referred to by asterisks, daggers, and so forth. The value of the editor's annotations have been enhanced by using, wherever possible, actual quotations from the works of the authorities concerned. The translations from von Frisch represent the most adequate account of his work which has yet appeared in English.

The few interpolations by the editor in the text are distinguished by square brackets. Lubbock's own list of references has been transferred from the beginning to the close of his text, while a short working bibliography of recent works on ants, bees, and wasps has been added. In compiling this reference-list, it has been borne in mind that a copious bibliography of ants in general is supplied in Wheeler's work of 1910, on British ants in Donisthorpe (1927), and very useful ones on all social insects in Wheeler (1923 and 1928).

The present edition of Lubbock is intended as an introduction to the more comprehensive works of Wheeler, Forel, and Donisthorpe. With that end in view, it has been necessary to avoid unduly enlarging it. This has been effected by omitting the more or less raw experimental data contained in Appendices A, B, C, D (part), E, and F. Appendix H and the summary of D have been inserted in the appropriate parts of the text, while Appendix G, consisting largely of Lubbock's own annotations, first published in the *Journal of the Linnean Society*,* has been split up and incorporated in the same series as the editor's notes, and referred to in the same way by numbers in the text, though credited in every case to Lubbock. Descriptions of new species, of which a few occurred in Appendix F, have been omitted, as presenting little interest in a work of this character. The plan of the new book is thus essentially simple—Lubbock's text without appendices, but followed by one consecutive series of annotations and a short working bibliography. There is also a brief introductory note on Lubbock as an entomologist and animal psychologist.

In the nomenclature of the ants mentioned by Lubbock changes have been made only where strictly necessary, and where the old name was quite out-of-date and misleading. Thus *Atta* in Lubbock's sense is now *Messor*, while his *Œcodoma* is *Atta*. Recent sub-genera have not been used.

Lubbock's five coloured plates have been replaced by new ones painted by Mr. A. J. E. Terzi, whose skill in insect portraiture needs no recommendation from an editorial pen.

* Observations on ants, bees, and wasps, pt. xi. *Jl. Linn. Soc. Zool.*, xx, 1887.

J. G. Myers.

LUBBOCK AS AN ENTOMOLOGIST AND COMPARATIVE PSYCHOLOGIST

By J. G. Myers

How doth the Banking Busy Bee
Improve the shining hours,
By studying on Bank Holidays
Strange insects and wild flowers.
from *Punch*, August, 1883.
" Life of Sir John Lubbock," vol. i, p. 199.

John Lubbock, afterwards Lord Avebury, was born in London in 1834. His long life was passed in that most prosperous period of British history when the fruit of the industrial revolution had ripened but had not yet begun to decompose. Though his circumstances were among the most comfortable in a comfortable age, his beginning work in the family bank at the early age of fifteen bred in him habits of industry which led to solid achievement in many spheres and enabled him to escape the futility of the wealthy dilettante. In his scientific work an early contact and lifelong friendship with Darwin was undoubtedly a paramount influence. This gave him above all his viewpoint as a natural selectionist, for he was in no sense a profound thinker.*

In estimating Lubbock's work the critic is compelled to divide it into compartments much as Lubbock himself divided the hours and quarter hours of his days. If we make watertight compartments ; so also did Lubbock, in whom it would seem, the anthropologist influenced

* In " writing on educational subjects ", says Sadler, " Lord Avebury takes his place in the English tradition. That tradition is attractively unpretentious, racy, idiomatic ; but unsystematized, and full of gaps. It has the weakness as well as the safety of being unphilosophical, even deliberately unphilosophical. And yet, underlying its cheerful stoicism and sturdy distaste for the abstract, there is, after all, something like a philosophy, toughly rooted in concealed presuppositions." The same might be said of his entomological writings.

but little the entomologist or the politician. Thus he took no academic anthropological theories with him into Parliament, nor adopted there " the professorial pose which is generally fatal to influence in any assembly of Englishmen " (Mallet). In spite of his extensive knowledge of ants and of men, he missed practically entirely, or at least failed to develop the immense importance of the comparative study of animal and human sociology.

We are here concerned only with Lubbock's investigations on insects and on animal behaviour.* There can be no doubt that in his biological researches he took Charles Darwin—his Master, as he called him—as a grand exemplar. Darwin wrote a purely systematic monograph on an obscure group of animals, the barnacles ; Lubbock did the same with those highly neglected insects, the Collembola and Thysanura. Darwin wrote on the expression of the emotions in man and animals, Lubbock on the behaviour of dogs, insects, and other forms. Both were keenly interested in the relations between flowers and insects. From his parents Lubbock received a religious faith which formed his moral character, and from Darwin a theory of evolution which guided all his scientific inquiries. Both he retained without material alteration to his death.

In anatomy and taxonomy Lubbock's contributions were of solid worth, and have not yet been superseded. His monograph of the Collembola and Thysanura is still the chief authority on the structure and classification of a difficult but increasingly important group of insects. His work on the anatomy of ants is very detailed ; " his dissections, and the exquisite drawings by which they were illustrated, having never been surpassed " (Donisthorpe). Lubbock was the first to find chordotonal (or supposed auditory) organs, in the legs of ants. " He

* More comprehensive accounts of his life and work, with adequate bibliographies, will be found in the following books : Hutchinson, H. G., 1914, *Life of Sir John Lubbock, Lord Avebury*, 2 vols., London ; various writers, edited by the Hon. Mrs. A. G. Duff, 1924, *The life work of Lord Avebury (Sir John Lubbock)*, London.

pointed out their resemblance to the sub-genual chordotonal organs of Orthoptera, discovered by von Siebold in 1844, but although he fancied he could discern some of their minute structure, his account and figure are very primitive" (Wheeler, 1910, p. 63).

One of his most interesting contributions to insect anatomy was his discovery of the so-called "internal gland" of scale-insects (Coccidæ), a complex arrangement of the digestive tract occurring in analogous though not homologous form in a number of other Homoptera, and enabling these insects to deal with the surplus water and (or) sugars of the plant sap which they imbibe.

In insect biology two problems, to which Lubbock devoted a small book, are of perennial interest. These are, firstly, the origin of insectan metamorphosis, and secondly the origin of the insects themselves. In seeking to explain the structure of many insect larvæ as adaptations to their own special environment, and mode of life, Lubbock was undoubtedly sound. As to the origin of insects, we know now not a whit more than when Lubbock's book appeared in 1874. There is fairly general agreement that modern insects are descended from a *Campodea*-like form, as Lubbock suggested, but beyond that is a mist of theory and controversy.

We come now to Lubbock's researches in animal behaviour. Since the present volume contains fairly copious annotations on his experiments with ants, bees, and wasps, we deal here only with general conclusions. Donisthorpe admirably sums up the work on ants :—

"He was the first observer to attain precision in experiment . . . by marking individual insects ; to confine ants between glass plates containing earth ; to observe ants' nests for long periods ; to keep individual ants alive for many years ; to witness the foundation of a colony from the egg ; to produce females in captivity ; to prove that the eggs of Aphides were carried by ants into their nests for the winter, and, when hatched in the spring, taken out and placed on their proper food-plants ; that ants are sensitive to . . . ultra-violet rays . . . ; etc."

And in the same volume J. Arthur Thomson writes : " We have seen that Lord Avebury had what might be called a characteristically *dynamic* view of Nature. He did his share of anatomy and histology, species-making, and classification, but what he cared for most was the creature *alive.*"

It is Thomson's conviction " that the greatest of the many services that Lord Avebury rendered to zoology was in being *a pioneer of the experimental study of animal behaviour* ". In this, however, a much greater than he, Henri Fabre, was many years before him ; while a century earlier still Réaumur's outlook was essentially experimental.

It seems to us that Thomson was nearer the mark in stressing Lubbock's interest in the insect as a living creature. It was Lubbock's supreme contribution, the basis of his psychological achievement, that he got to know individual insects intimately. It was a triumph of technique. When an ant died which he had kept for many years, the French paper which had a paragraph " profoundly sympathizing with the great scientist on the loss of his aged and valued relative ", showed unconsciously, perhaps, as much insight as humour. This attitude, this treatment of experimental animals as personalities, was justified in its results, and we venture to prophesy, will be increasingly justified in the progress of animal psychology.* It saved Lubbock from the Scylla of regarding insects as mere reflex machines ; while his own meticulous observations steered him reasonably clear of the Charybdis of anthropomorphism. It is probable that the animal psychology of the future will find less to criticize in Lubbock's conception of insect behaviour than in that of many of his successors, who deal in such dubious notions as " reversed behaviour " and " forced movements ". Even his anti-Bergsonian heresy

* Cf. the work of von Frisch on bees and of Köhler on apes.

that the "mental powers" of ants "differ from those of men not so much in kind as in degree", probably hardly deserves the criticism given it by J. Arthur Thomson, who writes: "Now Lord Avebury was very well aware . . . of these limitations of instinct, but he did not draw the conclusion which seems clear to many naturalists of to-day that instinctive behaviour and intelligent behaviour are on quite different evolution-tacks. There is no reason to believe that instinctive behaviour is a sort of low-grade form of intelligent behaviour, and there is little reason to believe that instinct is due to 'lapsed intelligence'." Perhaps not, but there are good grounds for thinking with McDougall * that "Instinct and Intelligence represent neither two divergent lines of evolution nor two stages of evolution, but rather are always only two aspects of all mental life which we distinguish by an effort of abstraction", an effort which Lubbock, studying his insects as individuals, and their activities as wholes, did not find it necessary to make.

One of the most remarkable features of Lubbock's works is their extraordinary popularity. He was by no means a "poet of science", he had none of Fabre's fire nor beauty; yet his biographer was able to write: "For that type of all popular ignorance, 'the man in the street,' the name of Sir John Lubbock is associated, in the first instance, no doubt, with the Bank Holidays, but in the second with the 'Ants, Bees, and Wasps', about which he published a very delightful and widely-read volume a little later. The idea of this man of business and of legislature poring over the small and hurrying insects struck the fancy of the people by its apparent paradox. It gave them one idea the more of the extraordinarily varied outlook and interest of the gifted man, who was himself of a remarkably ant-like industry . . . At this period of his varied career it is indeed evident that the aspect of his multitudinous industry which was impressing itself most vividly on the popular imagination was his

* *An outline of psychology*, London, 3rd edition, 1926, p. 202.

study of the intelligence of the hymenopterous insects. For the time being, at all events, it was over-shadowing all that he had done in antiquarian research, in other branches of science, in finance, or in social legislation."

It is probably true that more than half the pleasure of research with him lay in communicating the results to others. As Mallet says : " Knowledge was not an ultimate end with him ; he was not primarily a student but a man of affairs ; and quite as strong in him as love of knowledge was his desire to share it with others, and make it subservient to practical objects in improving the social and economic condition of his fellow men."

So far as entomology is concerned he amply avenged, at least in his own generation, the memory of Lady Glanville, " which had like to have suffered " for her devotion to entomology.* He was the last of the great Victorian amateurs. With the white man's increasing exploitation of every corner of the globe, and with the realization that insects are his greatest rivals, their relations with men are now taking on a sterner aspect, and this with the immense growth of entomology itself, will probably prevent any future amateur from attaining to the eminence that was Lubbock's.

* " . . . the ingenious Lady Glanvil, whose Memory had like to have suffered for her Curiosity. Some Relations that was (sic) disappointed by her Will, attempted to set it aside by Acts of Lunacy, for they suggested that none but those who were deprived of their Senses, would go in Pursuit of Butterflies. Her Relations and Legatees subpœnaed Dr. Sloan and Mr. Ray to support her Character. The last Gentleman went to Exeter, and on the Tryal satisfied the Judge and Jury of the Lady's laudable Inquiry into the wonderful Works of the Creation, and established her Will. She not only made the Study of Insects Part of her Amusement, but was as curious in her Garden, and raised an Iris from the Seed, which is known to this Day, by Miss Glanvil's Flaming Iris." Moses Harris, *The Aurelian : or Natural History of English Insects* . . . London, 1766, p. 34.

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ANTS, BEES, AND WASPS

CHAPTER I

INTRODUCTION

The Anthropoid apes no doubt approach nearer to man in bodily structure than do any other animals; but when we consider the habits of Ants, their social organization, their large communities, and elaborate habitations; their roadways, their possession of domestic animals, and even, in some cases, of slaves, it must be admitted that they have a fair claim to rank next to man [1] in the scale of intelligence. They present, moreover, not only a most interesting, but also a very extensive field of study.

Ants are divided into three families: the Formicidæ, Poneridæ, and Myrmicidæ, comprising many genera and a large number of species.[2] In this country we have rather more than thirty kinds; but ants become more numerous in species, as well as individuals, in warmer countries, and more than a thousand species are known.[3] Even this large number is certainly far short of those actually in existence.*

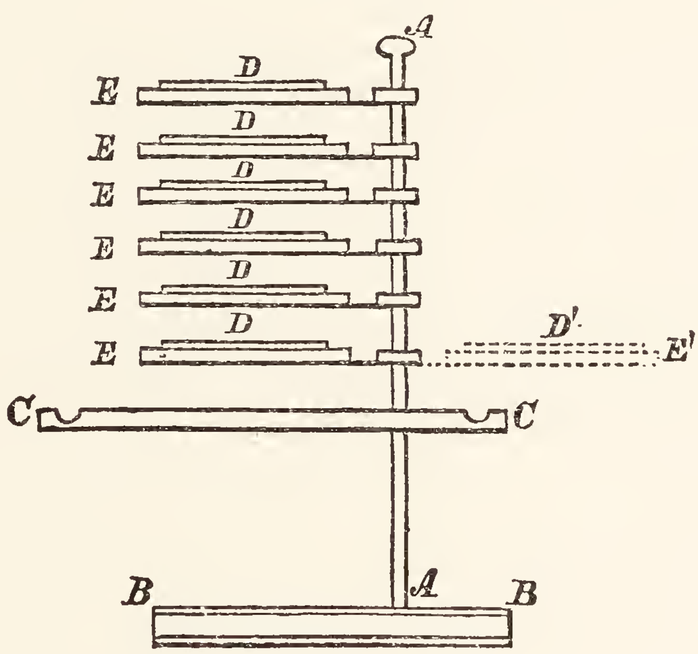
I have kept in captivity about half of our British species of ants, as well as a considerable number of foreign forms, and for the last few years have generally had from thirty to forty communities under observation.

* I have had some doubt whether I should append descriptions of the British species. On the whole, however, I have not thought it necessary to do so. They are well given in various entomological works: for instance, in Smith's *Cat. of British Fossorial Hymenoptera*, published by the Trustees of the British Museum; Saunders' "Synopsis of British Heterogyna", *Trans. Entomological Soc. London*; and in Mayr's *Die Europ. Formiciden*, all of which are cheap and easily procurable. I have, however, given figures of the principal species with which I have worked. [See reading-list.—Ed.]

After trying various plans, I found the most convenient method was to keep them in nests[4] (see Fig. 2, p. 33) consisting of two plates of common window glass, about ten inches square, and at a distance apart of from $\frac{1}{10}$ to $\frac{1}{4}$ of an inch (in fact just sufficiently deep to allow the ants freedom of motion), with slips of wood round the edges, the intermediate space being filled up with fine earth. If the interval between the glass plates was too great, the ants were partly hidden by the earth, but when the distance between the plates of glass was properly regulated with reference to the size of the ants, they were open to close observation, and had no opportunity of concealing themselves. Ants, however, very much dislike light in their nests, probably because it makes them think themselves insecure, and I always therefore kept the nest covered over, except when under actual observation. I found it convenient to have one side of the nest formed by a loose slip of wood, and at one corner I left a small door. These glass nests I either kept in shallow boxes with loose glass covers resting on baize, which admitted enough air, and yet was impervious to the ants; or on stands surrounded either by water, or by fur with the hairs pointing downwards. Some of the nests I arranged on stands, as shown in Fig. 1. A A is an upright post fixed on a base B B. C C is a square platform of wood round which runs a ditch of water. Above are six nests, D, each lying on a platform E, which could be turned for facility of observation, as shown in the dotted lines D′ and E′. Thus the ants had a considerable range, as they could wander as far as the water ditch. The object of having the platform C C larger than the supports of the nests was that if the ants fell, as often happened, they were within the water boundary, and were able to return home. This plan answered fairly well, and saved space, but it did not quite fulfil my hopes, as the ants were so pugnacious, that I was obliged to be very careful which nests were placed on the same stand.

Of course it is impossible to force the ants into these glass nests. On the other hand, when once the right way is known, it is easy to induce them to go in. When I wished to start a new nest I dug one up, and brought home the ants, earth, etc., all together. I then put them over one of my artificial nests, on one of the platforms surrounded by a moat of water. Gradually the outer earth dried up, while that between the two plates of glass, being protected from evaporation, retained its moisture. Under these circumstances the ants found it more suitable to their requirements, and gradually

Fig. 1.



deserted the drier mould outside, which I removed by degrees. In the earth between the plates of glass the ants tunnelled out passages, chambers, etc. (Fig. 2, p. 33), varying in form according to the circumstances and species.

Even between the plates of glass the earth gradually dried up, and I had to supply artificial rain from time to time. Occasionally also I gave them an altogether new nest. They seem, however, to get attached to their old homes, and I kept one community in the same glass case from 1874 till 1890.

It is hardly necessary to say that the individual ants belonging to the communities placed on the stands just described, knew their own nests perfectly well.

These nests gave me special facilities for observing the internal economy of ant life. Another main difference between my observations and those of previous naturalists has consisted in the careful record of the actions of individual ants. The most convenient mode of marking the ants was, I found, by placing a small dab of paint on the back, and, in the case of bees or wasps, by snipping off a fragment at the extremity of the wing. This, I need hardly say, from the structure of the wing, gives the insect no pain; in fact, as it is only necessary to remove a minute portion, not sufficient to make any difference in their flight, they seemed scarcely to notice it. I never found any difficulty in painting bees or wasps; if they are given a little honey they become so intent that they quietly allow the paint to be applied. Of course, too much must not be put on, and care must be taken not to touch the wings or cover up the spiracles. Ants require somewhat more delicate treatment, but with a little practice they could also be marked without any real difficulty.

No two species of Ants are identical in habits; and, on various accounts, their mode of life is far from easy to unravel. In the first place, most of their time is passed underground: all the education of the young, for instance, is carried on in the dark. Again, ants are essentially gregarious; it is in some cases difficult to keep a few alive by themselves in captivity, and at any rate their habits under such circumstances are entirely altered. If, on the other hand, a whole community is kept, then the greater number introduces a fresh element of difficulty and complexity. Moreover, even individuals of the same species seem to differ in character, and the same individual will behave very differently under different circumstances. Although, then, ants have attracted the attention of many of the older naturalists—Gould, De Geer, Réaumur, Swammerdam, Latreille, Leuwenhoeck, Huber—and have recently been the object of interesting observations by Frederick Smith, Belt, Moggridge, Bates, Mayr, Emery, Forel, McCook, and others, they still present one of the most promising fields for observation and experiment.

The life of an ant falls into four well-marked periods—those of the egg, of the larva or grub, of the pupa or chrysalis, and of the perfect insect or imago. The eggs are white or yellowish, and somewhat elongated. They are hatched about fifteen days after being laid. Those observed by me have taken a month or six weeks.

The larvæ [5] of ants, like those of bees and wasps, are small, white, legless grubs, somewhat conical in form, narrowing towards the head. They are carefully tended and fed, being carried about from chamber to chamber by the workers, probably in order to secure the most suitable amount of warmth and moisture. I have observed, also, that they are very often assorted according to age. It is sometimes very curious in my nests to see them arranged in groups according to size, so that they remind one of a school divided into five or six classes.

As regards the length of life of the larvæ, Forel supposed * that those of *Tapinoma* matured the quickest, and were full-grown in about six or seven weeks. Some of *Myrmica ruginodis*, however, observed by me, turned into pupæ in less than a month. In other cases the period is much longer. In certain species, *Lasius flavus*, for instance, some of the larvæ live through the winter.

When full grown the larvæ turn into pupæ, sometimes naked, sometimes covered with a silken cocoon, constituting the so-called "ant-eggs". We do not yet understand why some larvæ spin cocoons, while others remain naked. As a general rule, the species which have not a sting, are enveloped in a cocoon, while those which have, are naked. Latreille was the first to observe that in one species (*F. fusca*) the larvæ sometimes spin a cocoon, and

* *Les Fourmis de la Suisse*, p. 420.

sometimes remain naked. The reason for this difference is still quite unknown. After remaining some days in this state they emerge as perfect insects. In many cases, however, they would perish in the attempt, if they were not assisted, and it is very pretty to see the older ants helping them to extricate themselves, carefully unfolding their legs and smoothing out the wings, with truly feminine tenderness and delicacy. Our countryman, Gould, long ago mentioned, and the fact has since been fully confirmed by Forel, that the pupæ are unable to emerge from the cocoons without the assistance of the workers.[6] The ants generally remain from three to four weeks in this condition.

In the case of ants, as with other insects which pass through similar metamorphoses, such as bees, wasps, moths, butterflies, flies, and beetles, etc., the larval stage is the period of growth. During the chrysalis stage, though immense changes take place, and the organs of the perfect insect are more or less rapidly developed, no food is taken, and there is no addition to the size or weight.

The imago or perfect insect again takes food, but does not grow. The ant, like all the insects above named, is as large when it emerges from the pupa as it ever will be, though the abdomen of the females sometimes increases in size from the development of the eggs.

We have hitherto had very little information as to the length of life in ants in the imago, or perfect, state. So far, indeed, as the preparatory stages are concerned, there is little difficulty in approximately ascertaining the facts; namely, that while in summer they take only a few weeks, in some species, as our small yellow meadow ants (*Lasius flavus*), the autumn larvæ remain with comparatively little change throughout the winter. It is much more difficult to ascertain the length of life of the perfect insect, on account of their gregarious habits, and the difficulty of recognizing individual ants. I have found, however, as we shall presently see, that their life is much longer than has been generally supposed.

It is generally stated in entomological works that the males of ants die almost immediately. No doubt this is generally the case. At the same time, some males of *Myrmica ruginodis*, which I isolated with their mates in August, 1876, lived until the following spring; one of them till 17th May.

It has also been the general opinion that the females lived about a year. Christ * indeed thought they might last three or even four seasons, but this was merely a suggestion, and Forel expressed the general opinion when he said: "Je suis persuadé qu'en automne il ne reste presque plus que les ouvrières écloses pendant le courant de l'été." The average life of a queen is also, he thinks, not more than twelve months. I have found, however, that the life of the queens and workers is much longer than had been supposed. I shall give further details in a subsequent chapter, but I may just mention here that I kept a queen of *Formica fusca* from December, 1874, till August, 1888, when she must have been nearly fifteen years old, and, of course, may have been more.[7] She attained, therefore, by far the greatest age of any insect on record. †

I have also some workers which I have had since 1875.

The body of an ant consists of three parts: the head, thorax, and abdomen. The head bears the principal organs of sense, and contains the brain, as the anterior portion of the nervous system may fairly be called. The thorax, supporting the legs, and, when they are present, the wings, contains the principal muscles of locomotion. The abdomen contains the stomach and intestines, the organs of reproduction, the sting, etc.

Returning to the head: the antennæ consist of a short spherical basal piece, a long shaft, known as the

* *Naturgeschichte der Insekten.*

† Having reference to the facts stated on p. 37, this is a result of great physiological interest.

scape, and a flagellum of from six to seventeen (generally, however, from ten to thirteen) short segments, the apical ones sometimes forming a sort of club. The number of segments is generally different in the males and females.

The eyes are of two kinds. Large compound eyes, one on each side of the head; and ocelli, or so-called simple eyes. The compound eyes consist of many facets. The number differs greatly in different species, and in the different sexes, the males generally having the greatest number. Thus, in *Formica pratensis* there are, according to Forel, in the males about 1,200 in each eye, in the fertile females between 800 and 900, in the workers about 600. Where the workers vary in size they differ also in the number of facets. Thus, again following the same authority, the large workers of *Camponotus ligniperdus* have 500, the smaller ones only 450; while in the Harvesting ant (*Messor barbarus*) the contrast is even greater, the large specimens having 230, the small ones only from 80 to 90. The ordinary workers have in *Polyergus rufescens* about 400; in *Lasius fuliginosus*, 200; in *Tapinoma erraticum*, 100; in *Plagiolepis pygmæa*, 70 to 80; in *Lasius flavus*, about 80; in *Bothriomyrmex meridionalis*, 55; in *Strongylognathus testaceus*, *Stenamma westwoodi*, and *Tetramorium cæspitum*, about 45; in *Pheidole pallidula*, about 30; *Myrmecina latreillei*, 15; *Solenopsis fugax*, 6 to 9; while in *Ponera coarctata* there are only from 1 to 5; in *Eciton* only 1; and in *Typhlopone* the eyes are altogether wanting.

The number of facets seems to increase rather with the size of the insect than with the power of vision.

The ocelli are never more than three in number, disposed in a triangle with the apex in front. Sometimes the anterior ocellus alone is present. In some species the workers are altogether without ocelli, which, however, are always present in the queens and in the males.

The mouth parts are the labrum, or upper lip; the first pair of jaws or mandibles; the second pair of jaws or maxillæ, which are provided with a pair of palpi, or feelers; and the lower lip, or labium, also bearing a pair of palpi.

The thorax is generally considered to consist, as in other insects, of three divisions—the prothorax, mesothorax, and metathorax. I have elsewhere, however, given reasons into which I will not at this moment enter, for considering that the first abdominal segment has in this group coalesced with the thorax. The thorax bears three pairs of legs, consisting of a coxa, trochanter, femur, tibia and tarsus, the latter composed of five segments and terminating in a pair of strong claws.

In the males and females the meso- and meta-thorax each bear a pair of wings, which, however, in the case of the female, are stripped off by the insects themselves soon after the marriage flight.

The workers never possess wings, nor do they show even a rudimentary representative of these organs. Dr Dewitz has, however, pointed out that the full-grown larvæ of the workers possess well-developed "imaginal disks", like those which, in the males and females, develop into the wings. These disks, during the pupal life, gradually become atrophied, until in the perfect insects they are represented only by two strongly chitinized points lying under the large middle thoracic spiracles. No one unacquainted with the original history of these points would ever suspect them to be the rudimentary remnants of ancestral wings.*

The thorax also bears three pairs of spiracles, or breathing holes.

The abdomen consists of six segments,[8] in the queens and workers, that is to say in the females, and seven in the males. In the Formicidæ the first segment, as a general rule, forms a sort of peduncle (known as the scale or knot) between the metathorax and the remainder of the abdomen. In the Myrmicidæ two segments are thus detached from the rest.

The Poneridæ form, as regards the peduncle, and

* *Zeitschrift f. wiss. Zool.*, vol. xxviii, p. 555.

in some other respects, an intermediate group between the Formicidæ and the Myrmicidæ. The second abdominal segment is contracted posteriorly, but not so much so as to form a distinct knot.

The form of the knot offers in many cases valuable specific characters.

I am disposed to correlate the existence of a second knot among the Myrmicidæ with their power of stinging, which is wanting in the Formicidæ. Though the principal mobility of the abdomen is given in the former, as in the latter, by the joint between the metathorax and the knot, still the second segment of the peduncle must increase the flexibility, which would seem to be a special advantage to those species which have a sting.

It has indeed been said that Œcophylla has a sting, while it has only a single knot. Forel, however, has shown that the sting of Œcophylla is really rudimentary. It affords, therefore, no argument against my suggestion.

The knot is provided with a pair of spiracles, which are situated, as Forel states, in the front of the segment, and not behind, as supposed by Latreille.

In most entomological works it is stated that the Myrmicidæ have a sting, and that, on the contrary, the Formicidæ do not possess one. The latter family, indeed, possess a rudimentary structure representing the sting, but it seems merely to serve as a support for the poison duct. Dr Dewitz, who has recently published * an interesting memoir on the subject, denies that the sting in Formicidæ is a reduced organ, and considers it rather as in an undeveloped condition. The ancestors of our existing Ants, in his opinion, had a large poison apparatus, with a chitinous support like that now present in Formica, from which the formidable weapon of the bees, wasps, and Myrmicidæ have been gradually developed. I confess that I am rather disposed, on the contrary, to regard the condition of the organ in Formica

* *Zeitsch. f. wiss. Zool.*, vol. xxviii, p. 527.

as a case of retrogression contingent upon disuse.* I find it difficult to suppose that organs—so complex, and yet so similar—as the stings of ants, bees, and wasps, should have been developed independently.

Any opinion expressed by M. Dewitz on such a subject is, of course, entitled to much weight ; nevertheless there are some general considerations which seem to me conclusive against his view. If the sting of Formica represents a hitherto undeveloped organ, then the original ant was stingless, and the present stings of ants have an origin independent of that belonging to the other aculeate Hymenoptera, such as bees and wasps. These organs, however, are so complex, and at the same time so similarly constituted, that they must surely have a common origin. Whether the present sting is derived from a leaf-cutting instrument, such as that from which the sawfly takes its name, I will at present express no opinion. Dr Dewitz himself regards the rudimentary traces of wings in the larvæ of ants as the remnants of once highly-developed organs ; why, then, should he adopt the opposite view with reference to the rudimentary sting ? On the whole, I must regard the ancestral ant as having possessed a sting, and consider that the rudimentary condition of that of Formica is due to atrophy, perhaps through disuse.[9]

On the other hand, it is certainly, at first sight, difficult to understand why ants, having once acquired a sting, should allow it to fall into desuetude. There are, however, some considerations which may throw a certain light on the subject. The poison glands are much larger in Formica than in Myrmica. Moreover, some species have the power of ejecting their poison to a considerable distance. In Switzerland, after disturbing a nest of *Formica rufa*, or some nearly allied species, I have found that a hand held as much as 18 inches above the ants was covered with acid. But even when the poison

* This view has subsequently been adopted by Dr Beyer, *Jena Zeitsch.*, 1890.

is not thus fired at the enemy from a distance, there are two cases in which the sting might be allowed to fall into disuse. Firstly, those species which fight with their mandibles might find it on the whole most convenient to inject the poison (as they do) into the wounds thus created. Secondly, if the poison itself is so intensified in virulence as to act through the skin, a piercing instrument would be of comparatively small advantage. I was amused one day by watching some specimens of the little *Cremastogaster sordidula* and the much larger *Formica cinerea.* The former were feeding on some drops of honey, which the Formicas were anxious to share, but the moment one approached, the little Cremastogasters simply threatened them with the tip of their abdomen, and the Formicas immediately beat a hasty retreat. In this case the comparatively large Formica could certainly have had nothing to fear from physical violence on the part of the little Cremastogaster. Mere contact with the poison, however, appeared to cause them considerable pain, and generally the threat alone was sufficient to cause a retreat.

However this may be, in their modes of fighting, different species of ants have their several peculiarities. Some also are much less military than others. *Myrmecina latreillei*, for instance, never attack, and scarcely even defend themselves. Their skin is very hard, and they roll themselves into a ball, not defending themselves even if their nest is invaded; to prevent which they make the entrances small, and often station at each a worker, who uses her head to stop the way. The smell of this species is also, perhaps, a protection. *Tetramorium cæspitum* has the habit of feigning death. This species, however, does not roll itself up, but merely applies its legs and antennæ closely to the body.

Formica rufa, the common Horse ant, attacks in serried masses, seldom sending out detachments, while single ants scarcely ever make individual attacks. They rarely pursue a flying foe, but give no quarter, killing as many enemies as possible, and never hesitating, with this object, to sacrifice themselves for the common good.

Formica sanguinea, on the contrary, at least in their slave-making expeditions, attempt rather to terrify than to kill. Indeed, when invading a nest, they do not attack the flying inhabitants unless these are attempting to carry off pupæ, in which case the *F. sanguinea* force them to abandon the pupæ. When fighting, they attempt to crush their enemies with their mandibles.

Formica exsecta is a delicate, but very active species. They also advance in serried masses, but in close quarters they bite right and left, dancing about to avoid being bitten themselves. When fighting with larger species they spring on to their backs, and then seize them by the neck or by an antenna. They also have the instinct of acting together, three or four seizing an enemy at once, and then pulling different ways, so that she on her part cannot get at any one of her foes. One of them then jumps on her backs and cuts, or rather saws, off her head. In battles between this ant and the much larger *F. pratensis*, many of the *F. exsecta* may be seen on the backs of the *F. pratensis*, sawing off their heads from behind.

The species of *Lasius* make up in numbers what they want in strength. Several of them seize an enemy at once, one by each of her legs or antennæ, and when they have once taken hold they will suffer themselves to be cut in pieces rather than leave go.

Polyergus rufescens, the celebrated slave-making or Amazon ant, has a mode of combat almost peculiar to herself. The jaws are very powerful and pointed. If attacked—if, for instance, another ant seizes her by a leg—she at once takes her enemy's head into her jaws, which generally makes her quit her hold. If she does not, the *Polyergus* closes her mandibles, so that the points pierce the brain of her enemy, paralysing the nervous system. The victim falls in convulsions, setting free her terrible foe. In this manner a comparatively small force of *Polyergus* will fearlessly attack much larger armies of other species, and suffer themselves scarcely any loss.

Under ordinary circumstances an ants' nest, like a beehive, consists of three kinds of individuals : workers, or imperfect females (which constitute the great majority), males, and perfect females. There are, however, often several queens in an ants' nest ; while, as we all know, there is never more than one queen mother in a hive. The queens of ants are provided with wings, but after a single flight they tear them off, and do not again quit the nest. In addition to the ordinary workers there is in some species a second, or rather a third, form of female. In almost any ants' nest we may see that the workers differ more or less in size. The amount of difference, however, depends upon the species. In *Lasius niger*, the small brown garden ant, the workers are, for instance, much more uniform than in the little yellow meadow ant, or in *Messor barbarus*, where some of them are much more than twice as large as others. But in certain ants there are differences still more remarkable. Thus, in a Mexican species, *Myrmecocystus*,* besides the common workers, which have the form of ordinary neuter ants, there are certain others in which the abdomen is swollen into an immense sub-diaphanous sphere. These individuals are very inactive, and serve principally as living honey-jars. I have described in an earlier edition a species of *Camponotus* from Australia, which presents us with the same remarkable phenomenon. In the genus *Pheidole*, very common in southern Europe, there are also two distinct forms without any intermediate gradations ; one with heads of the usual proportion, and a second with immense heads provided with very large jaws. This differentiation of certain individuals so as to adapt them to special functions seems to me very remarkable ; for it must be remembered that the difference is not one of age or sex. The large-headed individuals are generally supposed to act as soldiers, and the size of the head

* Wesmael, *Bull. Acad. Roy. Bruxelles*, vol. v, p. 771.

enables the muscles which move the jaws to be of unusual dimensions; but the little workers are also very pugnacious. Indeed, in some nests of *Pheidole megacephala,* which I had for some time under observation, the small workers were quite as ready to fight as the large ones.

Again, in the genus *Colobopsis* Emery discovered that two ants, then supposed to be different species, and known as *Colobopsis truncata* and *C. fuscipes,* are really only two forms of one species. In this case the entrance to the nest is guarded by the large-headed form, which may therefore fairly be called a soldier.[10]

Savage observed among the Driver Ants, where also there are two kinds of workers, that the large ones arranged themselves on each side of the column formed by the small ones. They acted, he says, evidently the part of guides rather than of guards. At times they place "their abdomen horizontally on the ground, and laying hold of fixed points with their hind feet (which together thus acted as a fulcrum), elevate the anterior portion of their bodies to the highest point, open wide their jaws, and stretch forth their antennæ, which for the most part were fixed, as if in the act of listening and watching for approaching danger. They would occasionally drop their bodies to the ground again, run off to one side, and fiercely work their jaws and antennæ, as if having detected some strange sounds in the distance. Discerning nothing, they would quickly return to their posts and resume their positions, thus acting as scouts".*

The same thing has been noticed by other naturalists. Bates, for instance, states that in the marching columns of *Eciton hamatum,* the large-headed workers "all trotted along empty-handed and outside the column, at pretty regular intervals from each other, like subaltern officers in a marching regiment. . . . I did not see them change their position, or take any notice of their

* Rev. T. S. Savage on the "Habits of the Driver Ants", *Trans. Ent. Soc.,* vol. v, p. 12.

small-headed comrades" ; and he says that if the column was disturbed they appeared less pugnacious than the others.

In another species, however, of the same genus, *Eciton cœcum,* which also has two distinct kinds of workers, the ones with large heads do appear to act mainly as soldiers. When a breach is made in one of their covered ways, the small workers set to work to repair the damage, while the large-headed ones issue forth in a menacing manner, rearing themselves up and threatening with their jaws.

In the Sauba Ant of South America (*Atta cephalotes*), the complexity is carried still further ; Lund * pointed out that there were two different kinds of workers, but Bates has since shown that there are in this species no less than five classes of individuals, namely : (1) males ; (2) queens ; (3) small ordinary workers ; (4) large workers, with very large hairy heads ; (5) large workers, with large polished heads. Bates never saw either of these two last kinds do any work at all, and was not able to satisfy himself as to their functions. They have also been called soldiers, but this is obviously a misnomer—at least, they are said never to fight. Bates suggests † that they may "serve, in some sort, as passive instruments of protection to the real workers. Their enormously large, hard and indestructible heads may be of use in protecting them against the attacks of insectivorous animals. They would be, on this view, a kind of *pièces de resistance,* serving as a foil against onslaughts made on the main body of workers".

This does not, I confess, appear to me a probable explanation of the fact, and on the whole it seems that the true function of these large-headed forms is not yet satisfactorily explained.[11]

The question then arises whether these different kinds of workers are produced from different eggs.

* *Ann. des Sci. Nat.*, 1831, p. 122.
† Loc. cit., p. 31.

I am disposed to concur with Westwood in the opinion * "that the inhabitants of the nest have the instinct so to modify the circumstances producing this state of imperfection, that some neuters shall exhibit characters at variance with those of the common kind". This, indeed, credits them with a very remarkable instinct, and yet I see no more probable mode of accounting for the facts. Moreover, the exact mode by which the differences are produced is still entirely unknown.[12]

M. Forel, in his excellent work on ants, has pointed out that very young ants devote themselves at first to the care of the larvæ and pupæ, and that they take no share in the defence of the nest or other out-of-door work until they are some days old. This seems natural, because at first their skin is comparatively soft; and it would clearly be undesirable for them to undertake rough work or run into danger until their armour had had time to harden. There are, however, reasons for thinking that the division of labour is carried still further. I do not allude merely to those cases in which there are completely different kinds of workers, but even to the ordinary workers. In *L. flavus*, for instance, it seems probable that the duties of the small workers are somewhat different from those of the large ones, though no such division of labour has yet been detected. I shall have to record some further observations pointing in the same direction.

The nests of ants may be divided into several classes. Some species, such as our common Horse ant (*Formica rufa*), collect large quantities of materials, such as bits of stick, fir leaves, etc., which they heap up into conical masses. Some construct their nests of earth, the cells being partly above, partly below, the natural level. Some are entirely underground, others eat into the trunks of old trees.

In warmer climates the variations are still more numerous. *Dolichoderus bispinosus*, of Cayenne, forms its

* *Modern Classification of Insects*, vol. ii, p. 225.

nest of the cottony matter from the capsules of Bombax. Sykes has described * a species of *Myrmica* which builds in trees and shrubs, the nest consisting of thin leaves of cow-dung, arranged like tiles on the roof of a house ; the upper leaf, however, covering the whole.

In some cases the nests are very extensive. Bates mentions that while he was at Pará an attempt was made to destroy a nest of the Sauba ants by blowing into it the fumes of sulphur, and he saw the smoke issue from a great number of holes, some of them not less than seventy yards apart.

A community of ants must not be confused with an ant hill in the ordinary sense. Very often indeed a community has only one dwelling, and in most species seldom more than three or four. Some, however, form numerous colonies. M. Forel even found a case in which one nest of *F. exsecta* had no less than two hundred colonies, and occupied a circular space with a radius of nearly two hundred yards. Within this area they had exterminated all the other ants, except a few nests of *Tapinoma erraticum*, which survived, thanks to their great agility. In these cases the number of ants thus associated together must have been enormous. Even in single nests Forel estimates the numbers at from five thousand to half a million.

Ants also make for themselves roads. These are not merely worn by the continued passage of the ants, as has been supposed, but are actually prepared by the ants, rather however by the removal of obstacles, than by any actual construction, which would indeed not be necessary, the weights to be carried being so small. In some cases these roadways are arched over with earth, so as to form covered ways. In others, the ants excavate regular subterranean tunnels, sometimes of considerable length. The Rev. Hamlet Clark even assures us that he observed one in South America, which passed under the river Parahyba at a place where it was as

* *Trans. Ent. Soc.*, vol. i.

broad as the Thames at London Bridge. I confess, however, that I have my doubts as to this case, for I do not understand how the continuity of the tunnel was ascertained.

The food of ants consists of insects, great numbers of which they destroy ; of honey, honeydew, and fruit : indeed, scarcely any animal or sweet substance comes amiss to them. Some species, such, for instance, as the small brown garden ant (*Lasius niger*), ascend bushes in search of aphides. The ant then taps the aphis gently with her antennæ, and the aphis emits a drop of sweet fluid, which the ant drinks. Sometimes the ants even build covered ways up to and over the aphides, which, moreover, they protect from the attacks of other insects.[13] Our English ants do not store up provision for the winter ; indeed, their food is not of a nature which would admit of this. I have indeed observed that the small brown ant sometimes carries seeds of the violet into its nest, but for what purpose is not clear.[14] Some of the southern ants, however, lay up stores of grain (see Chapter III).

Ants have many enemies. They themselves, and still more their young, are a favourite food of many animals. They are attacked also by numerous parasites. If a nest of the brown ants is disturbed at any time during the summer, some small flies may probably be seen hovering over the nest, and every now and then making a dash at some particular ant. These flies belong to the genus *Phora*,[15] and to a species hitherto unnamed, which Mr Verrall has been good enough to describe for me. They lay their eggs on the ants, inside which the larvæ live. Other species of the genus are in the same way parasitic on bees. Ants are also sometimes attacked by mites. On one occasion I observed that one of my ants had a mite attached to the underside of its head. The mite, which maintained itself for more than three months in the same position, was almost as large as the head. The ant could not remove it herself. Being a queen, she did not come out of the nest, so that I could not do it for her, and none of her own companions thought of performing this kind office.

In character the different species of ants differ very much from one another. *F. fusca,* the one which is pre-eminently the "slave" ant, is, as might be expected, extremely timid; while the nearly allied *F. cinerea* has, on the contrary, a considerable amount of individual audacity. *F. rufa,* the horse ant, is, according to M. Forel, especially characterized by the want of individual initiative, and always moves in troops; he also regards the genus *Formica* as the most brilliant; though others excel it in other respect as, for instance, in the sharpness of their senses. *F. pratensis* worries its slain enemies; *F. sanguinea* never does so. The slave-making ant (*P. rufescens*) is perhaps the bravest of all. If a single individual finds herself surrounded by enemies, she never attempts to fly, as any other ant would, but transfixes her opponents one after another, springing right and left with great agility, till at length she succumbs, overpowered by numbers. *M. scabrinodis* is cowardly and thievish: during wars among the larger species they haunt the battlefields and devour the dead. *Tetramorium* is said to be very greedy; *Myrmecina* very phlegmatic.[16]

In industry ants are not surpassed even by bees and wasps. They work all day, and in warm weather, if need be, even at night too. I once watched an ant from six in the morning, and she worked without intermission till a quarter to ten at night. I had put her to a saucer containing larvæ, and in this time she carried off no less than a hundred and eighty-seven to the nest. I kept another ant, which I employed in my experiments, under continuous observation several days. When I started for London in the morning, and again when I went to bed at night, I used to put her in a small bottle, but the moment she was let out she began to work again. On one occasion I was away from home for a week. On my return I took her out of the bottle, placing her on a little heap of larvæ about three feet from the nest. Under these circumstances I certainly did not expect her to return. However, though she had thus been six days in confinement, the brave little creature immediately picked up a larva, carried it off to the nest, and after half an hour's rest returned for another.

Our countryman Gould noticed * certain "amusements" or "sportive exercises" which he had observed among ants. Huber also mentions † scenes which he had witnessed on the surface of ant hills, and which, he says, "I dare not qualify with the title gymnastic, although they bear a close resemblance to scenes of that kind." The ants raised themselves on their hind legs, caressed one another with their antennæ, engaged in mock combats, and almost seemed to be playing hide and seek. Forel entirely confirms Huber's statements, though he was at first incredulous. He says ‡ :—

"Malgré l'exactitude avec laquelle il décrit ce fait, j'avais peine à y croire avant de l'avoir vu moi-même, mais une fourmilière pratensis m'en donna l'exemple à plusieurs reprises lorsque je l'approchai avec précaution. Des ☿ (i.e. workers) se saisissaient par les pattes ou par les mandibules, se roulaient par terre, puis se retachaient, s'entraînaient les unes les autres dans les trous de leur dôme pour en ressortir aussitôt après, etc. Tout cela sans aucun acharnement, sans venin ; il était évident que c'était purement amical. Le moindre souffle de ma part mettait aussitôt fin à ces jeux. J'avoue que ce fait peut paraître imaginaire à qui ne l'a pas vu, quand on pense que l'attrait des sexes ne peut en être cause."

Bates, also, in the case of *Eciton legionis*, observed behaviour which looked to him, "like simple indulgence in idle amusement, the conclusion," he says, "that the ants were engaged merely in play was irresistible." § [17]

* *An Account of English Ants*, p. 103.
† *Nat. Hist. of Ants*, p. 197.
‡ Loc. cit., p. 367.
§ Loc. cit., vol. ii, p. 362.

Lastly, I may observe that ants are very cleanly animals, and assist one another in this respect. I have often seen them licking one another.[18] Those, moreover, which I painted for facility of recognition were gradually cleaned by their friends.

CHAPTER II

ON THE FORMATION AND MAINTENANCE OF NESTS, AND ON THE DIVISION OF LABOUR

It is remarkable that notwithstanding the researches of so many excellent observers, and though ants' nests swarm in every field and every wood, we did not know how their nests commence.

Three principal modes have been suggested.[19] After the marriage-flight the young queen may either :—

(1) Join her own or some other old nest ;

(2) Associate herself with a certain number of workers, and with their assistance commence a new nest ; or

(3) Found a new nest by herself.

The question can, of course, only be settled by observation, and the experiments made to determine it had hitherto been indecisive.

Blanchard, indeed, in his work on *The Metamorphoses of Insects* (I quote from Dr Duncan's translation, p. 205), says : "Huber observed a solitary female go down into a small underground hole, take off her own wings, and become, as it were, a worker ; then she constructed a small nest, laid a few eggs, and brought up the larvæ by acting as mother and nurse at the same time."

This, however, is not a correct version of what Huber says. His words are : "I enclosed several females in a vessel full of light humid earth, with which they constructed lodges, where they resided, some singly, others in common. They laid their eggs and took great care of them ; and notwithstanding the inconvenience of not being able to vary the temperature of their habitation, they reared some, which became larvæ of a tolerable size, but which soon perished from the effect of my own negligence." *

It will be observed that it was the eggs, not the larvæ,

* *Natural History of Ants*, Huber, p. 121.

which, according to Huber, these isolated females reared. It is true that he attributes the early and uniform death of the larvæ to his own negligence, but the fact remains that in none of his observations did an isolated female bring her offspring to maturity.

Other entomologists, especially Forel and Ebrard, have repeated the same observations with similar results; and as yet in no single case had an isolated female been known to bring her young to maturity. Forel even thought himself justified in concluding, from his observations and from those of Ebrard, that such a fact could not occur.

Lepeletier de St. Fargeau * was of opinion that ants' nests originate in the second mode indicated above, and it is, indeed, far from improbable that this may occur. No clear case has, however, yet been observed. M. de St Fargeau himself observes † that "les particularités qui accompagnent la formation première d'une fourmilière sont encore incertaines et mériteraient d'être observées avec soin".

Under these circumstances I made the following experiments:—

(1*a*) I took an old fertile queen from a nest of *Lasius flavus*, and put her to another nest of the same species. The workers became very excited and attacked her.

(*b*) I repeated the experiment, with the same result.

(*c*) Do. do. In this case the nest to which the queen was transferred was without a queen; still they would not receive her.

(*d*) and (*e*) Do. do. do.

I conclude, then, that at any rate in the case of *L. flavus*, the workers will not adopt an old queen from another nest.

The following observation shows that, at any rate in some cases, isolated queen ants are capable of giving origin to a new community.

* *Hist. Nat. des Ins. Hyménoptères*, vol. i, p. 143.
† *Hist. Nat. des Ins. Hyménoptères*, vol. i, p. 144.

On 14th August, 1876, I isolated two pairs of *Myrmica ruginodis* which I found flying in my garden. I placed them with damp earth, food, and water, and they continued perfectly healthy through the winter. In April one of the males died, and the second in the middle of May. The first eggs were laid between 12th and 23rd April. They began to hatch the first week in June, and the first larva turned into a chrysalis on the 27th; a second on the 30th; a third on 1st July, when there were also seven larvæ and two eggs. On the 8th there was another egg. On 8th July a fourth larva had turned into a pupa. On 11th July I found there were six eggs, and on the 14th about ten. On the 15th one of the pupæ began to turn brown, and the eggs were about fifteen in number. On the 16th a second pupa began to turn brown. On the 21st a fifth larva had turned into a pupa, and there were about twenty eggs. On 22nd July the first worker emerged and a sixth larva had changed. On the 25th I observed the young worker carrying the larvæ about when I looked into the nest; a second worker was coming out. On 28th July a third worker emerged, and a fourth on 5th August. The eggs appeared to be less numerous, and some had probably been devoured.

This experiment shows that the queens of *Myrmica ruginodis* have the instinct of bringing up larvæ and the power of founding communities. The workers remained about six weeks in the egg, a month in the state of larvæ, and twenty-five to twenty-seven days as pupæ.

Since, however, cases are on record in which communities are known to have existed for many years, it seems clear that fresh queens must be sometimes adopted. I have indeed recorded several experiments in which fertile queens introduced into queenless nests were ruthlessly attacked, and subsequent experiments have always had the same result. Mr Jenner Fust, however, suggested to me to introduce the queen into the nest, as is done with bees, in a wire cage, and leave her there for two or three days, so that the workers might, as it were, get accustomed to her. Accordingly I procured a queen of *F. fusca* and put her with some honey in a queenless nest, enclosed in a wire cage so that the ants could not get at her. After three days I let her out, but she was at once attacked. Perhaps I ought to have waited a few days longer. On the contrary, Mr McCook reports a case of the adoption of a fertile queen of *Cremastogaster lineolata* by a colony of the same species * : "The queen," he says, "was taken 16th April, and on 14th May following was introduced to workers of a nest taken the same day. The queen was alone within an artificial glass formicary, and several workers were introduced. One of these soon found the queen, exhibited much excitement but no hostility, and immediately ran to her sister workers, all of whom were presently clustered upon the queen. As other workers were gradually introduced they joined their comrades, until the body of the queen (who is much larger than the workers) was nearly covered with them. They appeared to be holding on by their mandibles to the delicate hairs upon the female's body, and continually moved their antennæ caressingly. This sort of attention continued until the queen, escorted by workers, disappeared in one of the galleries. She was entirely adopted, and thereafter was often seen moving freely, or attended by guards, about the nest, at times engaged in attending the larvæ and pupæ which had been introduced with the workers of the strange colony. The workers were fresh from their own natural home, and the queen had been in an artificial home for a month."

In no case, however, when I have put a queen into one of my nests has she been accepted.

Possibly the reason for the difference may be that the ants on which I experimented had been long living in a republic ; for, I am informed, that if bees have been

* *Proc. Acad. Natural Sciences of Philadelphia*, 1879. "Note on the Adoption of an Ant-Queen," by Mr McCook, p. 139.

long without a queen it is impossible to induce them to accept another.

Moreover, I have found that when I put a queen with a few ants from a strange nest they did not attack her, and by adding others gradually, I succeeded in securing the throne for her.

It is generally stated that among ants the queens only lay eggs. This, however, is not correct.

Denny * and Lespès † have shown that the workers also are capable of producing eggs ; but the latter asserted that these eggs never come to maturity. Forel, however, has proved ‡ that this is not the case, but that in some cases, at any rate, the eggs do produce young. Dewitz even maintains § that the workers habitually lay eggs, and explains the difference which on this view exists between the workers of ants and those of bees, on the ground that (as he supposes) the majority of ants die in the autumn, so that the eggs laid by the queens alone would not be sufficient to stock the nest in the spring ; while among bees the majority survive the winter, and consequently the eggs laid by the queen are sufficient to maintain the numbers of the community. In reply to this argument, it may be observed that among wasps the workers all perish in the autumn, while, on the contrary, among ants I have proved that, at least as regards many species, this is not the case. Moreover, although eggs are frequently laid by workers, this is not so often the case as Dewitz appears to suppose. Forel appears to have only observed it in one or two cases. In my nests the instances were more numerous ; and, indeed, I should say that in most nests there were a few fertile workers.

Among bees and wasps also the workers are occasionally fertile ; but, so far as our observations go, it is a curious fact that their eggs never produce females, either queens or workers, but always males. The four or five specimens

* *Ann. and Mag. Nat. Hist.*, 2nd ser., vol. i.
† *Ann. des Sci. Nat.*, 1863.
‡ *Fourmis de la Suisse*, p. 329.
§ *Zeitsch. f. wiss. Zool.*, vol. xxviii, p. 536.

bred by Forel from the eggs of workers were, moreover, all males.

It became therefore an interesting question whether the same is the rule among ants; and my nests have supplied me with some facts bearing on the question. Most of my nests contained queens; and in these it would be impossible, or at least very difficult, to distinguish and follow the comparatively few eggs laid by the workers. Some of my nests, however, contained no queen; and in them therefore all the eggs must have been laid by workers.

One of these was a nest of *Formica cinerea*, which I brought back from Castellamare in November, 1875. At that time it contained no eggs or larvæ. In 1876 a few eggs were laid of which fifteen came to maturity and were, I believe, all males. In 1877 there were fourteen pupæ, of which twelve came to maturity, and were all males.

Again, in a nest of *Lasius niger*, kept in captivity since July, 1875, there were in 1876 about 100 young; and these were, as far as I could ascertain, all males. At any rate, there were about 100 males, and I could not find a single young female. In 1877 there were again some pupæ; but owing to an accident none of them came to maturity. In 1878 fifteen came to maturity; and fourteen were males. The other I could not find after it left the pupa skin; but I have no doubt, from the appearance of the pupa, that it was also a male.

Another nest of *Lasius niger*, taken in November, 1875, brought in 1878 only one young ant to maturity; and this was a male.

Again, in a nest of *Formica fusca*, taken in 1875, though in 1876 and 1877 eggs were laid and a few arrived at the pupa-state, none came to maturity. They were all, however, either males or queens, and, I have little doubt, were males. In 1878 one came to maturity, and it was a male.

A nest of *F. fusca*, captured in 1876, did not bring up any young in 1877. In 1878 three larvæ came to maturity; and they all proved to be males. Another nest of *F. fusca*, captured in 1877, in 1878 brought only one young one to maturity. This was a male.

In the following year (1879) I again carefully watched my nests, to see what further light they would throw on the subject.

In six of those which contained no queen, eggs were produced, which of course must necessarily have been laid by workers.

In the first of these, the nest of *Lasius niger*, which I have watched since July, 1875, and which, therefore is interesting from the great age of the workers, about ten larvæ were hatched, but only four reached the pupa state. Of these one disappeared; the other three I secured, and on examination they all proved to be males. The nest of *Lasius niger*, which has been under observation since November, 1875, produced about ten pupæ. Of these I examined seven, all of which I found to be males. The others escaped me. I believe that, having died, they were brought out and thrown away.

The nest of *Formica cinerea*, captured at the same time, produced four larvæ, all of which perished before arriving at the pupa stage. The larvæ of males and of queens are much larger than those of the workers, and, these larvæ were too big to have been those of workers.

In a nest of *Formica fusca* which I have had under observation since August, 1876, three pupæ were produced. They were all males. Another nest of *Formica fusca* produced a single young one, which also was a male.

Lastly, my nest of *Polyergus rufescens*, which M. Forel was so good as to send me in the spring of 1876, in 1879 produced twelve pupæ. Eleven of these turned out to be males. The other one I lost; and I have little doubt that it was brought out and thrown away. It was certainly not a worker. As regards the first three of these pupæ, I omitted to record at the time whether they belonged to the *Polyergus* or to the slaves, though I have little doubt that they belonged to the former species. The last eight, at any rate, were males of *Polyergus*.

Indeed, in all of my queenless nests, males have been produced ; and in not a single queenless nest has a worker laid eggs which have produced a female, either a queen or a worker. Perhaps I ought to add that workers are abundantly produced in those of my nests which possess a queen.

While great numbers of workers and males have come to maturity in my nests, with one exception not a single queen has been produced.

This was in a nest of *Formica fusca*, in which five queens came to maturity. The nest (which, I need hardly say, possessed a queen) had been under observation since April, 1879, and the eggs therefore must have been laid in captivity. The nest had been richly supplied with animal food, which may possibly account for the fact.

It is known that bees, by difference of food, etc., possess the power of obtaining at will from the same eggs either queens or ordinary workers. Mr Dewitz,* however, is of opinion that among ants, on the contrary, the queens and workers are produced from different kinds of eggs. He remarks that it is very difficult to understand how the instinct, if it is to be called instinct, which would enable the working ants to make this difference can have arisen. This is no doubt true ; but it seems to me quite as difficult to understand how the queens, which must have originally laid only queen eggs and male eggs, can have come to produce another class. Moreover, however great the difficulty may be to understand how the ants can have learnt to produce queens and workers from one kind of egg, the same difficulty exists almost to the same extent in bees, which, as Mr Dewitz admits, do possess the power. Moreover, it seems to me

* *Zeitsch. für wiss. Zool.*, 1878, p. 101.

very unlikely that the result is produced in one way in the case of bees, and in another in that of ants. It is also a strong argument that in none of my nests, though thousands of workers and males have been produced, had I ever observed a queen to be so until the year 1879. On the whole, then, though I differ from so excellent a naturalist with much hesitation, I cannot but think that ants, like bees, possess the power of developing a given egg into either a queen or a worker [see Note 12].

I have already mentioned that the previous views as to the duration of life of ants turn out to be quite erroneous. It was the general opinion that they lived for a single year. Two of my queen ants lived, the one nearly fourteen, the other nearly fifteen years, viz. from December, 1874, to July, 1887, and August, 1888, respectively. During the whole time they enjoyed perfect health, and every year have laid eggs producing workers, a fact which suggests physiological conclusions of great interest.

I have, moreover, little doubt that some of the workers now in this nest were among those originally captured, the mortality after the first few weeks having been but small. This, however, I cannot prove.

A nest of *F. sanguinea*, which M. Forel kindly forwarded to me on 12th September, 1875 (but which contained no queen), gradually diminished in numbers, until in February, 1879, it was reduced to two *F. sanguinea* and one slave. The latter died in February, 1880. One of the two mistresses died between 10th May and 16th May, 1880, and the other only survived her a few days, dying between the 16th and 20th. These two ants, therefore, must have been five years old at least. It is certainly curious that they should, after living so long, have died within ten days of one another. There was nothing, as far as I could see, in the state of the nest or the weather to account for this, and they were well supplied with food ; yet I hardly venture to suggest that the survivor pined away for the loss of her companion.

Some workers of *F. cinerea* lived in one of my nests from November, 1875, to April, 1882.

Workers of *F. fusca* have attained the age of six years in several of my nests, and in one of *Lasius niger* brought in on 30th November, 1875, there were no queens; and, as already mentioned, no workers have been produced. Those now living (February, 1883) are therefore the original ones, and they must be more than seven years old.

The duration of life in ants is therefore much greater than has been hitherto supposed.

Though I lose many ants from accidents, especially in summer, in winter there are very few deaths.

I have given the following figures (Fig. 2 and Pl. VI) which represent a typical nest belonging to *Lasius niger*, because it is a good instance of the mode in which my ants excavated chambers and galleries for themselves, and seems to show some ideas of strategy. The nest is, as usual, between two plates of glass, the outer border is a framework of wood, and the shaded part represents garden mould, which the ants have themselves excavated, as shown in the figure. For the small doorway (*a*), indeed, I am myself responsible. I generally made the doorways of my nests narrow, so as to check evaporation and keep the nests from becoming too dry. It will be observed, however, that behind the hall (*b*) the entrance contracts, and is still further protected by a pillar of earth, which leaves on either side a narrow passage which a single ant could easily guard, or which might be quickly blocked up. Behind this is an irregular vestibule (*c*), contracted again behind into a narrow passage, which is followed by another, this latter opening into the main chamber (*d*). In this chamber several pillars of earth are left, almost as if to support the roof. Behind the main chamber is an inner sanctum divided into three chambers, and to which access is obtained through narrow entrances (*f, f, f, f*). Most of the pillars in the main chamber are irregular in outline, but two of them (*g, g*) were regular ovals, and round each, for a distance about as long as the body of an ant, the glass had been most carefully cleaned. This was so marked, and the edge of the cleaned portion

FIG. 2.

Ground-plan of a typical nest of *Lasius niger*, reduced. *a*, narrow doorway; *b*, hall; *c*, vestibule; *d*, main chamber; *e*, inner sanctum; *f, f, f, f*, narrow entrance passages to sanctum; *g, g*, special pillars.

was so distinct, that it is impossible not to suppose that the ants must have had some object in this proceeding, though I am unable to suggest any explanation of it.

Figure 2 was made in 1880. Plate VI shows the same nest as it was in 1887. It will be seen that the general arrangement has altered but little in the six years. In this plate are represented the ants themselves, with their queen, and young in several stages; the larvæ, sorted as usual in several groups according to age, and the pupæ by themselves; and lastly two kinds of domestic animals, the little *Cyphodeirus* and the blind Woodlice. The insects are represented in their actual positions, but a little larger, in proportion to the nest, than they actually are. It will be observed that many of the ants are grouped round the queen, and all have their faces turned towards her. Plate V represents a fortified nest of another species. The circular camp is entered by gateways, which, however, are not visible in a view from above.

I have already mentioned (ante, p. 17) that there is evidence of some division of labour among ants. Where indeed there are different kinds of workers, this is self-evident, but even in species where the workers are all of one type, something of the same kind appears to occur.

In the autumn of 1875 I noticed an ant belonging to one of my nests of *F. fusca* out feeding alone. The next day the same ant was again out by herself, and for some weeks no other ant, so far as I observed, came out to the food. I did not, however, watch her with sufficient regularity. In the winter of 1876, therefore, I kept two nests under close observation, having arranged with my daughters and their governess, Miss Wendland (most conscientious observers), that one of us should look at them once an hour during the day. One of the nests contained about 200 individuals of *F. fusca*, the other was a nest of *P. rufescens* with the usual slaves, about 400 in number. The mistresses themselves never came out for food, leaving all this to the slaves.

We began watching on 1st November, but did not keep an hourly register till the 20th, after which date the results were given in tables (see Appendix *). Table No. 1 relates to the nest of *F. fusca,* and the ants are denoted by numbers. The hours at which we omitted to record an observation are left blank; when no ant was at the honey, the square is marked with a 0. An ant, marked in my register as No. 3, was at the time when we began observing acting as feeder to the community.

The only cases in which other ants came to the honey were at 2 p.m. on 22nd November, when another ant came out, whom we registered as No. 4, another on the 28th, registered as No. 5. Other ants came out occasionally, but not one came to the honey (except the above mentioned) from 28th November till 3rd January, when another (whom we registered as No. 6) began feeding. After this a friend visited the honey once on the 4th, once on the 11th, and again on the 15th, when she was registered as No. 7.

Table No. 2 is constructed in the same way, but refers to the nest of *Polyergus.* The feeders in this case were, at the beginning of the experiment, registered as Nos. 5, 6, and 7. On 22nd November, a friend, registered as No. 8, came to the honey, and again on 11th December; but with these two exceptions the whole of the supplies were carried in by Nos. 5 and 6, with a little help from No. 7.

Thinking now it might be alleged that possibly these were merely unusually active or greedy individuals, I imprisoned No. 6 when she came out to feed on the 5th. As will be seen from the table, no other ant had been out to the honey for some days; and it could therefore hardly be accidental that on that very evening another ant (then registered as No. 9) came out for food. This ant, as will be seen from the table, then took the place of No. 6, and (No. 5 being imprisoned on 11th January) took in all the supplies, again with a little help from No. 7. So matters continued till the 17th, when I imprisoned No. 9, and then again, i.e. on the 19th, another ant

* In earlier editions.—Ed.

(No. 10) came out for the food, aided, on and after the 22nd, by another, No. 11. This seems to me very curious. From 1st November to 5th January, with two or three casual exceptions, the whole of the supplies were carried in by three ants, one of whom, however, did comparatively little. The other two were imprisoned, and then, but not till then, a fresh ant appears on the scene. She carried in the food for a week; and then, she being imprisoned, two others undertook the task. On the other hand, in Nest 1, where the first foragers were not imprisoned, they continued during the whole time to carry in the necessary supplies.

The facts therefore certainly seem to indicate that certain ants are told off as foragers, and that during winter, when little food is required, two or three are sufficient to provide it.

I have, indeed, no reason to suppose that in our English ants any particular individuals are specially adapted to serve as receptacles of food. In some foreign species * certain individuals in each nest serve as animated honey-pots. To them the foragers bring their supplies, and their whole duty seems to be to receive the honey, retain it, and redistribute it when required. Their abdomen becomes enormously distended, the intersegmental membranes being so much extended that the chitinous segments which alone are visible externally in ordinary ants seem like small brown transverse bars. Two species presenting this remarkable peculiarity are known.[20] The first (*Myrmecocystus mexicanus*) was described by Wesmael from specimens brought home by M. de Normann, and the account given by them has been fully confirmed by subsequent observers; as, for instance, by Lucas,† Saunders,‡ Edwards,§ Blake,|| Loew,¶ and McCook.**

* *Bull. de l'Acad. des Sci. de Bruxelles*, vol. v, p. 771.
† *Ann. Soc. Ent. de France*, v, p. 111.
‡ *Canadian Entomologist*, vol. vii, p. 12.
§ *Proc. California Academy*, 1873.
|| Ibid., 1874.
¶ *American Nat.*, viii, 1874.
** *The Honey Ants.*

On one very important point, however, M. Wesmael was in error; he states that the abdomen of these abnormal individuals, "ne contient aucun organe; ou plutôt, il n'est lui-même qu'un vaste sac stomacal." Blake even asserts that "the intestine of the insect is not continued beyond the thorax", which must surely be a misprint; and also that there is no connexion between the stomach and the intestine! These statements, however, are entirely erroneous; and, as M. Forel has shown, the abdomen does really contain the usual organs, which, however, are very easily overlooked by the side of the gigantic crop.

I have therefore been much interested in receiving a second species of ant, which has been sent me by Mr Waller, in which a similar habit has been evolved and a similar modification has been produced. The two species, however, are very distinct, belonging to totally different genera; and the former is a native of Mexico, while the one now described comes from Adelaide in Australia. The two species, therefore, cannot be descended one from the other; and the conclusion seems inevitable that the modification has originated independently in the two species.*

It is interesting that, although these specimens apparently never leave the nest, and have little use therefore for legs, mandibles, etc., the modifications which they have undergone seem almost confined to the abdominal portion of the digestive organs. The head and thorax, antennæ, jaws, legs, etc., differ but little from those of ordinary ants.

* I have since received another species from Australia with the same peculiarity.

CHAPTER III

ON THE RELATION OF ANTS TO PLANTS

It is now generally admitted [21] that the form and colour, the scent and honey of flowers, are mainly due to the unconscious agency of insects, and especially of bees. Ants have not exercised so great an influence over the vegetable kingdom, nevertheless they have by no means been without effect.

The great object of the beauty, scent, and honey of flowers, is to secure cross fertilization; but for this purpose winged insects are almost necessary, because they fly readily from one plant to another, and generally confine themselves for a certain time to the same species. Creeping insects, on the other hand, naturally would pass from one flower to another on the same plant; and as Mr Darwin has shown, it is desirable that the pollen should be brought from a different plant altogether. Moreover, when ants quit a plant, they naturally creep up another close by, without any regard to species. Hence, even to small flowers, such as many crucifers, composites, saxifrages, etc., which, as far as size is concerned, might well be fertilized by ants, the visits of flying insects are much more advantageous. Moreover, if larger flowers were visited by ants, not only would they deprive the flowers of their honey without fulfilling any useful function in return, but they would probably prevent the really useful visits of bees. If you touch an ant with a needle or a bristle, she is almost sure to seize it in her jaws; and if bees, when visiting any particular plant, were liable to have the delicate tip of their proboscis seized on by the horny jaws of an ant, we may be sure that such a species of plant would soon cease to be visited. On the other hand, we know how fond ants are of honey, and how zealously and unremittingly they search for food. How is it then that they do not anticipate the bees, and secure the honey for themselves? This is guarded against in several ways.

Belt appears to have been the first naturalist to call attention to this interesting subject.

"Many flowers," he says,* "have contrivances for preventing useless insects from obtaining access to the nectaries.

. . . . .

"Great attention has of late years been paid by naturalists to the wonderful contrivances amongst flowers to secure cross fertilization, but the structure of many cannot, I believe, be understood, unless we take into consideration not only the beautiful adaptations for securing the services of the proper insect or bird, but also the contrivances for preventing insects that would not be useful from obtaining access to the nectar. Thus the immense length of the *Angræcum sesquipedale* of Madagascar might, perhaps, have been more easily explained by Mr Wallace, if this important purpose had been taken into account."

Kerner has since published a very interesting work,† especially devoted to the subject, which has been translated into English by Dr Ogle.

In aquatic plants, of course, the access of ants is precluded by the isolation in water. Nay, even many land plants have secured to themselves the same advantage, the leaves forming a cup round the stem. Some species have such a leaf-cup at each joint, in others there is only a single basin, formed by the rosette of radical leaves. In these receptacles rain and dew not only collect, but are retained for a considerable time. In our own country *Dipsacus sylvestris* (the common teazle) is the best marked instance of this mode of protection, though

* *The Naturalist in Nicaragua.* By Thos. Belt, pp. 131 and 133.
† Kerner, *Flowers and their Unbidden Guests.*

it is possible that these cups serve another purpose, and form, as suggested by Francis Darwin, traps in which insects are caught, and in which they are dissolved by the contained fluid, so as to serve as food for the plant. However this may be, the basins are generally found to contain water, even if no rain has fallen for some days, and must, therefore, serve to prevent the access of ants.

The next mode of protection is by means of slippery surfaces. In this case, also, the leaves often form a collar round the stem, with curved surfaces over which ants cannot climb. "I have assured myself," says Kerner, "not only by observation, but by experiment, that wingless insects, and notably ants, find it impossible to mount upwards over such leaves as these. The little creatures run up the stem, and may even not unfrequently traverse the under surface of the leaves, if not too smooth; but the reflexed and slippery margin is more than the best climbers among them can get over, and if they attempt it they invariably fall to the ground. There is no necessity for the lamina of the leaf to be very broad; even narrow leaves, as, for instance, those of *Gentiana verna*, are enough for the purpose, supposing, of course, that the margin is bent backwards in the way described."

Of this mode of protection the cyclamen and snowdrop offer familiar examples. In vain do ants attempt to obtain access to such flowers, the curved surfaces baffle them; when they come to the edge they inevitably drop off to the ground again. In fact, these pendulous flowers protect the honey as effectually from the access of ants, as the hanging nests of the weaver and other birds protect their eggs and young from the attacks of reptiles.

In a third series of plants the access of creeping insects is impeded or altogether prevented by certain parts of the flower being crowded together so as to leave either a very narrow passage or none at all. Thus the *Antirrhinum*, or snapdragon, is completely closed, and only a somewhat powerful insect can force its way in. The flower is in fact a strong box, of which the Humble-bee only has the key. The Linarias are another case of this kind. The Campanulas, again, are open flowers, but the stamens are swollen at the base, and in close contact with one another, so that they form the lid of a hollow box in which the honey is secreted. In some species the same object is effected by the stamens being crowded together, as in some of the white Ranunculuses of the Alps. In other cases, the flower forms a narrow tube, still further protected by the presence of hairs, sometimes scattered, sometimes, as in the white dead nettle, forming a row.

In others, as in some species of Narcissus, Primula, Pedicularis, etc., the tube itself is so narrow that even an ant could not force its way down.

In others, again, as in some of the Gentians, the opening of the tube is protected by the swollen head of the pistil.

In others, as in clover, lotus, and many other *Leguminosæ*, the ovary and the stamens, which cling round the ovary in a closely-fitting tube, fill up almost the whole space between the petals, leaving only a very narrow tube.

Lastly, in some, as in *Geranium robertianum*, *Linum catharticum*, etc., the main tube itself is divided by ridges into several secondary ones.

In still more numerous species the access of ants and other creeping insects is prevented by the presence of spines or hairs, which constitute veritable *chevaux de frise*. Often these hairs are placed on the flowers themselves, as in some verbenas and gentians. Sometimes the whole plant is more or less hairy and it will be observed that the hairs of plants have a great tendency to point downwards, which of course constitutes them a more efficacious barrier.

In another class of cases access to the flowers is prevented by viscid secretions. Everyone who has any acquaintance with botany knows how many species bear the specific name of "Viscosa" or "Glutinosa". We have, for instance, *Bartsia viscosa*, *Robinia viscosa*, *Linum viscosum, Euphrasia viscosa, Silene viscosa, Dianthus viscidus, Senecio viscosus, Holosteum glutinosum,* etc. Even those who have never opened a botanical work must have noticed how many plants are more or less sticky. Why is this? What do the plants gain by this peculiarity? The answer probably is, at any rate in most cases, that creeping insects are thus kept from the flowers. The viscid substance is found most frequently and abundantly on the peduncles immediately below the blossoms, or even on the blossoms themselves. In *Epimedium alpinum,* for instance, the leaves and lower parts of the stem are smooth, while the peduncles are covered with glandular, viscid hairs. The number of small insects which are limed and perish on such plants is very considerable. Kerner counted sixty-four small insects on one inflorescence of *Lychnis viscosa.* In other species the flower is viscid: as, for instance, in the gooseberry, *Linnæa borealis, Plumbago Europæa,* etc.

Polygonum amphibium is a very interesting case. The small rosy flowers are richly supplied with honey; but from the structure of the flower, it would not be fertilized by creeping insects. As its name indicates, this plant grows sometimes on land, sometimes in water. Those individuals, however, which grow on dry land are covered by innumerable glandular viscid hairs, which constitute an effectual protection. On the other hand, the individuals which grow in water are protected by their situation. To them the grandular hairs would be useless, and in fact on such specimens they are not developed.

In most of the cases hitherto mentioned the viscid substance is secreted by glandular hairs, but in others it is discharged by the ordinary cells of the surface. Kerner is even of opinion that the milky juice of certain plants—for instance, of some species of *Lactuca* (lettuce)—answers the same purpose. He placed several kinds of ants on these plants, and was surprised to find that their sharp claws cut through the delicate epidermis; while through the minute clefts thus made the milky juice quickly exuded, by which the ants were soon glued down. Kerner is even disposed to suggest that the nectaries which occur on certain leaves are a means of protection against the unwelcome, because unprofitable, visits of creeping insects, by diverting them from the flowers.

Thus, then, though ants have not influenced the present condition of the vegetable kingdom to the same extent as bees, yet they also have had a very considerable effect upon it in many ways.

Our European ants do not strip plants of their leaves. In the tropics, on the contrary, some species do much damage in this manner.

Bates considers * that the leaves are used " to thatch the domes which cover the entrances to their subterranean dwellings, thereby protecting them from the rains ". Belt, on the other hand, maintains that they are torn up into minute fragments, so as to form a flocculent mass, which serves as a bed for mushrooms ; the ants are, in fact, he says, " mushroom growers and eaters." †

Some trees are protected by one species of ants from others.[22] A species of Acacia, described by Belt, bears hollow thorns, while each leaflet produces honey in a crater-formed gland at the base, as well as a small, sweet, pear-shaped body at the tip. In consequence, it is inhabited by myriads of a small ant, which nests in the hollow thorns, and thus finds meat, drink, and lodging all provided for it. These ants are continually roaming over the plant ; and constitute a most efficient body-guard, not only driving off the leaf-cutting ants, but, in Belt's opinion, rendering the leaves less liable to be eaten by herbivorous mammalia. Delpino mentions that on one occasion he was gathering a flower of *Clerodendrum fragrans* when he was himself " suddenly attacked by a whole army of small ants ". ‡

* Loc. cit., v. i, p. 26.

† Loc. cit., p. 79. This view has since been confirmed by Schimper, *Bot. Mitt. aus den Tropen*, Nr. 6.

‡ *Scientific Lectures*, p. 33.

Moseley has also called attention * to the relations which have grown up between ants and two "curious epiphytes, *Myrmecodia armata* and *Hydnophytum formicarum*. Both plants are associated in their growth with certain species of ants. As soon as the young plants develop a stem, the ants gnaw at the base of this, and the irritation produced causes the stem to swell; the ants continuing to irritate and excavate the swelling, it assumes a globular form, and may become even larger than a man's head.

"The globular mass contains within a labyrinth of chambers and passages, which are occupied by the ants as their nest. The walls of these chambers and the whole mass of the inflated stem retain their vitality and thrive, continuing to increase in size with growth. From the surface of the rounded mass are given off small twigs, bearing the leaves and flowers.

"It appears that this curious gall-like tumour on the stem has become a normal condition of the plants, which cannot thrive without the ants. In *Myrmecodia armata* the globular mass is covered with spine-like excrescences. The trees I referred to at Amboina had these curious spine-covered masses perched in every fork, and with them also smooth surfaced masses of a species of *Hydnophytum*."

There are, of course, many cases in which the action of ants is very beneficial to plants. They kill off a great number of small caterpillars and other insects. Forel found in one large nest that more than twenty-eight dead insects were brought in per minute; which would give during the period of greatest energy more than 100,000 insects destroyed in a day by the inhabitants of one nest alone.

Our English hunting ants generally forage alone, but in warmer countries they hunt in packs, or even troops.

As already mentioned, none of our northern ants

* *Notes by a Naturalist on the "Challenger"*, p. 389.

store up grain, and hence there has been much discussion as to the well-known passage of Solomon. I have indeed observed that the small brown ants, *Lasius niger*, sometimes carry seeds of the violet into their nests, but for what purpose is not clear.[23] It is, however, now a well-established fact that more than one species of southern ants do collect seeds of various kinds. The fact, of course, has long been known in those regions.

Indeed, the quantity of grain thus stored up is sometimes so considerable, that in the "Mischna", rules are laid down with reference to it; and various commentators, including the celebrated Maimonides, have discussed at length the question whether such grain belonged to the owner of the land, or might be taken by gleaners—giving the latter the benefit of the doubt. He does not appear to have considered the rights of the ants.

Hope * has called attention to the fact that Meer Hassan Ali, in his *History of the Mussulmans*, expressly mentions this habit. "More industrious little creatures," he says, "cannot exist than the small red ants, which are so abundant in India. I have watched them at their labours for hours, without tiring. They are so small, that from eight to twelve in number labour with great difficulty to convey a grain of wheat or barley, yet these are not more than half the size of a grain of English wheat. I have known them to carry one of these grains to their nest, at a distance from 600 to 1,000 yards. They travel in two distinct lines over rough or smooth ground, as it may happen, even up and down steps, at one regular pace. The returning unladen ants invariably salute the burthened ones, who are making their way to the general storehouse; but it is done so promptly, that the line is neither broken nor their progress impeded by the salutation."

Sykes, in his account of an Indian ant, *Pheidole providens*,† appears to have been the first of modern

* *Trans. Ent. Soc.*, 1840, p. 213.
† Ibid., 1836, p. 99. Dr Lincecum has also made a similar observation.

scientific authors to confirm the statements of Solomon. He states that the above-named species collects large stores of grass seeds, on which it subsists from February to October. On one occasion he even observed the ants bringing up their stores of grain to dry them after the closing thunderstorms of the monsoon ; an observation which has been since confirmed by other naturalists.

It is now known that harvesting ants occur in the warmer part of Europe, where their habits have been observed with care, especially by Moggridge and Lespès. It does not yet seem quite clear in what manner the ants prevent the grains from germinating. Moggridge found that if the ants were prevented from entering the granaries, the seeds began to sprout, and that this was also the case in deserted granaries. It would appear, therefore, that the power of germination was not destroyed.[24]

On the other hand, Lespès confirms the statement long ago made by Pliny that the ants gnaw off the radicle, while Forel asserts that *Messor structor* allows the seeds in its granaries to commence the process of germination for the sake of the sugar.

A Texan ant, *Pogonomyrmex barbatus*, is also a harvesting species, storing up especially the grains of *Aristida oligantha*, the so-called "ant-rice", and of a grass, *Buchlœ dactyloides*. These ants clear disks, ten or twelve feet in diameter, round the entrance to their nest, a work of no small labour in the rich soil, and under the hot sun of Texas. I say "clear disks", but some, though not all, of these disks are occupied, especially round the edge, by a growth of ant rice. These ants were first noticed by Mr Buckley,* and their habits were some time afterwards described in more detail by Dr Lincecum,† who maintained not only that the ground was carefully cleared of all other species of plants, but that this grass was intentionally cultivated by the

* *Proc. Acad. Nat. Sci. Philadelphia*, 1860.
† *Linnean Journal*, 1861, p. 29.

ants. Mr McCook,* by whom this subject has been recently studied, fully confirms Dr Lincecum that the disks are kept carefully clean, that the ant rice alone is permitted to grow on them, and that the produce of this crop is carefully harvested; but he thinks that the ant rice sows itself, and is not actually cultivated by the ants.[25] I have myself observed in Algeria, that certain species of plants are allowed by the ants to grow on their nests.

* *The Nat. Hist. of the Agricultural Ants of Texas*, p. 88.

CHAPTER IV

ON THE RELATIONS OF ANTS TO OTHER ANIMALS

THE relations existing between ants and other animals are even more interesting than their relations with plants. As a general rule, not, however, without many remarkable exceptions, they may be said to be those of deadly hostility.

Though honey is the principal food of ants, they are very fond of meat, and in their wild state destroy large numbers of other insects. Our English ants generally go out hunting alone, but many of the species living in hotter climates hunt in packs, or even in troops.

Savage has given * a graphic account of the " Driver " ants (*Anomma arcens*, West.) of West Africa. They keep down, he says, " the more rapid increase of noxious insects and smaller reptiles; consume much dead animal matter, which is constantly occurring, decaying, becoming offensive, and thus vitiating the atmosphere, and which is by no means the least important in the Torrid Zone, often compelling the inhabitants to keep their dwellings, towns, and their vicinity in a state of comparative cleanliness. The dread of them is upon every living thing. . . .

" Their entrance into a house is soon known by the simultaneous and universal movement of rats, mice, lizards, Blapsidæ, Blattidæ, and of the numerous vermin that infest our dwellings. Not being agreed, they cannot dwell together, which modifies in a good measure the severity of the Drivers' habits, and renders their visits sometimes (though very seldom in my view) desirable. . . .

" They move over the house with a good degree of order, unless disturbed, occasionally spreading abroad,

* " On the Habits of the Driver Ants," *Trans. Ent. Soc.*, 1847, p. 14.

ransacking one point after another, till, either having found something desirable, they collect upon it, when they may be destroyed *en masse* by hot water. . . .

"When they are fairly in, we give up the house, and try to await with patience their pleasure, thankful, indeed, if permitted to remain within the narrow limits of our beds or chairs."

These ants will soon destroy even the largest animal if it is confined. In one case Savage saw them kill near his house a snake four feet long. Indeed, it is said that they have been known to destroy the great python, when gorged with food and powerless. The natives even believe that the python, after crushing its victim, does not venture to swallow it, until it has made a search, and is satisfied that there are no Drivers in the vicinity! It is very remarkable that these hunting ants are blind. They emerge, however, principally by night, and like some of the blind hunting ants of Brazil (*Eciton cæcum*), well described by Bates,* prefer to move under covered galleries, which they construct rapidly as they advance. "The column of foragers pushes forward step by step, under the protection of these covered passages, through the thickets, and on reaching a rotting log, or other promising hunting ground, pour into the crevices in search of booty."

The marauding troops of Ecitons may, in some cases, be described as armies. "Wherever they move," says Bates,† "the whole world is set in commotion, and every creature tries to get out of their way. But it is especially the various tribes of wingless insects that have cause for fear, such as heavy-bodied spiders, ants of other species, maggots, caterpillars, larvæ of cockroaches, and so forth, all of which live under fallen leaves or in decaying wood. The Ecitons do not mount very high on trees, and therefore the nestlings of birds are not much incommoded by them. The mode of operation of these armies, which I ascertained,

* *The Naturalist on the River Amazon*, vol. ii, p. 364.
† Ibid., p. 358.

only after long-continued observation, is as follows: The main column, from four to six deep, moved forward in a given direction, clearing the ground of all animal matter dead or alive, and throwing off, here and there, a thinner column to forage for a short time on the flanks of the main army, and re-enter it again after their task is accomplished. If some very rich place be encountered anywhere near the line of march—for example, a mass of rotten wood abounding in insect larvæ, a delay takes place, and a very strong force of ants is concentrated upon it."

Belt, also, has given * an excellent account of these Ecitons. He observed that spiders were peculiarly intelligent in escaping them, making off several yards in advance; and not like cockroaches and other stupider insects, taking shelter in the first hiding-place, where they were almost sure to be detected. The only chance of safety was either to run right away or to stand still. He once saw a Harvestman (*Phalangium*) standing in the midst of an army of ants with the greatest circumspection and coolness, lifting its long legs one after the other. Sometimes as many as five out of the eight would be in the air at once, but it always found three or four spots free from ants, on which it could safely place its feet. On another occasion, Belt observed a green leaf-like locust, which remained perfectly still, allowing the ants to run over it. This they did, but seem to have been quite deceived by its appearance and immobility, apparently taking it for a leaf.

In other cases, insects mimic ants, and thus escape attack or are able to stalk their prey. Belt mentions a spider which in its form, colour, and movements so much resembled an ant, that he was himself for some time deceived.[26]

Nor are ants without their enemies.[27] We all know how fond birds are of their larvæ and pupæ. They have also numerous parasites. I have already alluded to the mites which are often found in ants' nests. These are

* *The Naturalist in Nicaragua*, p. 17.

of several kinds; one of them, not uncommon in the nests of *Lasius flavus*, turned out to be a new species, and has been described for me by Mr Michael.

Certain species of Diptera, belonging to the family Phoridæ, are also parasitic on ants. As already mentioned, I forwarded specimens to Mr Verrall, who finds that some of them are a new species of the genus *Phora*, and that among them is also the type of a new genus, which he proposes to call *Platyphora*, doing me the honour of naming the species after me.

But the social and friendly relations which exist between ants and other animals are of a more complex and much more interesting character.

It has long been known that ants derive a very important part of their sustenance from the sweet juice excreted by aphides. These insects, in fact, as has been over and over again observed, are the cows of the ants; in the words of Linnæus, "Aphis formicarum vacca." A good account of the relations existing between ants and aphides was given more than a hundred years ago by the Abbé Boisier de Sauvages.*

Nor are the aphides the only insects which serve as cows to the ants. Various species of Beetles, Coccidæ, Cercopis,[28] Centrotus, Membracis, etc., are utilized in the same manner. H. Edwards † and McCook ‡ have observed ants licking the larva of a butterfly, *Lycæna pseudargiolus*.[29]

The different species of ants utilize different species of aphis. The common brown garden ant (*Lasius niger*) devotes itself principally to aphides which frequent twigs and leaves; *Lasius brunneus*, to the aphides which live on the bark of trees; while the little yellow ant (*Lasius flavus*) keeps flocks and herds of the root-feeding aphides.

In fact, to this difference of habit the difference of

* "Observations sur l'origine du miel," par l'Abbé Boisier de Sauvages, *Jour. de Physique*, vol. i, p. 187.

† *Canadian Entomologist*, January, 1878.

‡ *The Mound-making Ants of the Alleghanies*, p. 289.

colour is perhaps due. The Baltic amber contains among the remains of many other insects a species of ant intermediate between our small brown garden ants and the little yellow meadow ants. This is possibly the stock from which these and other allied species are descended. One is tempted to suggest that the brown species which live so much in the open air, and climb up trees and bushes, have retained and even deepened their dark colour; while others, such as *Lasius flavus*, the yellow meadow ant, which lives almost entirely below ground, has become much paler.

The ants may be said almost literally to milk the aphides; for, as Darwin and others have shown, the aphides generally retain the secretion until the ants are ready to receive it. The ants stroke and caress the aphides with their antennæ, and the aphides then emit the sweet secretion.[30]

As the honey of the aphides is more or less sticky, it is probably an advantage to the aphis that it should be removed. Nor is this the only service which ants render to them. They protect them from the attacks of enemies [see Note 13]; and not unfrequently even build cowsheds of earth over them. The yellow ants collect the root-feeding species in their nests, and tend them as carefully as their own young. But this is not all. The ants not only guard the mature aphides, which are useful, but also the eggs of the aphides, which, of course, until they come to maturity, are quite useless. These eggs were first observed by our countryman Gould, whose excellent little work on ants * has hardly received the attention it deserves. In this case, however, he fell into error. He states that "the queen ant" [he is speaking of *Lasius flavus*] "lays three different sorts of eggs, the slave, female, and neutral. The two first are deposited in the spring, the last in July and part of August; or, if the summer be extremely favourable, perhaps a little sooner. The female eggs are covered with a thin black

* *An Account of English Ants*, by the Rev. W. Gould, 1747, p. 36.

membrane, are oblong, and about the sixteenth or seventeenth part of an inch in length. The male eggs are of a more brown complexion, and usually laid in March ".

These dark eggs are not those of ants, but of aphides. The error is very pardonable, because the ants treat these eggs exactly as if they were their own, guarding and tending them with the utmost care. I first met with them in February, 1876, and was much surprised to find that the ants took great care of these brown bodies, carrying them off to the lower chambers with the utmost haste when the nest was disturbed. I brought some home with me and put them near one of my own nests, when the ants carried them inside. That year I was unable to carry my observations further. In 1877 I again procured some of the same eggs, and offered them to my ants, who carried them into the nest, and in the course of March I had the satisfaction of seeing them hatch into young aphides. Huber had observed certain egg-like bodies in ants' nests. These, however, were not in his opinion true eggs. On the contrary, he agreed with Bonnet, "that the insect, in a state nearly perfect, quits the body of its mother in that covering which shelters it from the cold in winter, and that it is not, as other germs are, in the egg surrounded by food by means of which it is developed and supported. It is nothing more than an asylum of which the aphides born at another season have no need; it is on this account some are produced naked, others enveloped in a covering. The mothers are not, then, truly oviparous, since their young are almost as perfect as they ever will be, in the asylum in which Nature has placed them at their birth." *

This is, I think, a mistake. I do not propose here to describe the anatomy of the aphis; but I may observe that I have examined the female, and find these eggs to arise in the manner described by Huxley,† and which

* *The Natural History of Ants*, by M. P. Huber, 1820, p. 246.
† *Linnean Transactions*, 1858.

I have also myself observed in other aphides and in allied genera.* Moreover, I have opened the eggs themselves, and have also examined sections, and have satisfied myself that they are really eggs containing ordinary yelk. So far from the young insect being " nearly perfect ", and merely enveloped in a protective membrane, no limbs or internal organs are present. In fact, the young aphis does not develop in them until shortly before they are hatched.†

In any case Huber supposed that they belonged to the aphides which live in the ants' nests. When my eggs hatched I naturally also thought that the aphides belonged to one of the species usually found on the roots of plants in the nests of *Lasius flavus.* To my surprise, however, the young creatures made the best of their way out of the nest, and, indeed, were sometimes brought out by the ants themselves. In vain I tried them with roots of grass, etc. ; they wandered uneasily about, and eventually died. Moreover, they did not in any way resemble the subterranean species. In 1878 I again attempted to rear these young aphides ; but though I hatched a great many eggs, I did not succeed. In 1879, however, I was more fortunate. The eggs commenced to hatch the first week in March. Near one of my nests of *Lasius flavus,* in which I had placed some of the eggs in question, was a glass containing living specimens of several species of plant commonly found on or around ants' nests. To this some of the young aphides were brought by the ants. Shortly afterwards I observed on a plant of daisy, in the axils of the leaves, some small aphides, very much resembling those from my nest, though we had not actually traced them continuously. They seemed thriving, and remained stationary on the daisy. Moreover,

* *Philosophical Transactions*, 1859.

† I do not enter here into the technical question of the difference between ova and pseudova. I believe these to be true ova, but the point is that they are not a mere envelope containing a young aphis, but eggs in the ordinary sense, the contents of which consist of yelk, and in which the young aphis is gradually developed.

whether they had sprung from the black eggs or not, the ants evidently valued them, for they built up a wall of earth round and over them. So things remained throughout the summer; but on the 9th October I found that the aphides had laid some eggs exactly resembling those found in the ants' nests; and on examining daisy-plants from outside, I found on many of them similar aphides, and more or less of the same eggs.

I confess these observations surprised me very much. The fact that Huber found eggs of aphides in ants' nests, though confirmed by Schmarda, did not attract so much notice as many of the other interesting facts which they have recorded; because if aphides are kept by ants in their nests, it seems only natural that their eggs should also occur. The above case, however, is much more remarkable. Here are aphides, not living in the ants' nests, but outside, on the leaf-stalks of plants. The eggs are laid early in October on the food-plant of the insect. They are of no direct use to the ants, yet they are not left where they are laid, exposed to the severity of the weather and to innumerable dangers, but are brought into their nests by the ants, and tended by them with the utmost care through the long winter months until the following March, when the young ones are brought out and again placed on the young shoots of the daisy. This seems to me a most remarkable case of prudence. Our ants may not perhaps lay up food for the winter; but they do more, for they keep during six months the eggs which will enable them to procure food during the following summer, a case of prudence unexampled in the animal kingdom.

The nests of our common yellow ant (*Lasius flavus*) contain in abundance four or five species of aphis, more than one of which appears to be as yet undescribed. In addition, however, to the insects belonging to this family, there are a large number of others which live habitually in ants' nests, so that we may truly say that our English ants possess a much greater variety of domestic animals than we do ourselves. Märkel satisfied himself that large nests of *Formica rufa* might contain at least a thousand of such guests * ; and I believe that the aphides in a large nest of *Lasius flavus* would often be even more numerous. André † gives a list of no less than 584 species of insects, which are habitually found in association with ants, and of which 542 are beetles.[31]

The association of some of these insects with ants may be purely accidental and without significance. In some of them no doubt the bond of union is merely the selection of similar places of abode ; in some few others the ants are victimized by parasites of which they cannot rid themselves. There are, for instance, the parasitic mites, and the small black fly, belonging to the genus Phora, which lays her eggs on ants, and which I have already mentioned. Then there are some insects, such as the caterpillar of that beautiful beetle, the rosechafer, which find a congenial place of residence among the collection of bits of stick, etc., with which certain species of ants make their nests.

Another class of ant guests are those which reside actually in the galleries and chambers of, and with, the ants, but which the latter never touch. Of these the commonest in England are a species allied to Podura, for which I have proposed the name Beckia [*Cyphodeirus*]. It is an active, bustling little being, and I have kept hundreds, I may say thousands, in my nests. They run about in and out among the ants, keeping their antennæ in a perpetual state of vibration. Another very common species is a white crustacean allied to the woodlouse, and enjoying the rather long name of *Platyarthrus hoffmanseggii*. André only mentions Platyarthrus as living with *Formica rufa*, *Myrmica scabrinodis*, and *Leptothorax acervorum*. I have found it also with *Lasius niger*, *L. flavus*, and *F. fusca*. It runs about, and is evidently at home, among the ants.

* *Beit. zur Kenntniss der unter Ameisen lebenden Insekten*, Märkel, *Germar's Zeitsch. f. Ent.*, 1841, p. 210.

† *Rev. et Mag. de Zool.*, 1874, p. 205.

Both *Platyarthrus* and *Cyphodeirus*, from living constantly in the dark, have become blind; I say "have become", because their ancestors no doubt had eyes. In neither of these cases have I ever seen an ant take the slightest notice of either of these insects. One might almost imagine they had the cap of invisibility.

It is certain that the ants intentionally (if I may so say) sanction the residence of these insects in their nests. An unauthorized interloper would be at once killed. I have, therefore, ventured to suggest that these insects may, perhaps, act as scavengers.

In other cases the association is more close, and the ants take the greatest care of their guests.

It appears that many of these insects produce a secretion which serves as food for the ants. This is certainly the case, for instance, with the curious blind beetle, Claviger (so called from its club-shaped antennæ), which is quite blind,* and appears to be absolutely dependent upon the ants, as Müller first pointed out. It even seems to have lost the power of feeding itself; at any rate, it is habitually fed by the ants, who supply it with nourishment as they do one another. Müller saw the ants caressing the beetles with their antennæ. The Clavigers have certain tufts of hairs at the base of the elytra, and Müller, whose observations have since been confirmed by subsequent entomologists, saw the ants take these tufts of hairs into their mouths and lick them, as well as the whole upper surface of the body, with apparently the greatest enjoyment. Grimm † has made a similar observation with reference to *Dinarda dentata*, another of these myrmecophilous beetles. He several times observed the ants licking the tuft of hairs at the end of the abdomen. Lespès ‡ has confirmed this. On one occasion he saw an ant feed a Lomechusa. Several of the former were sucking a

* *Germar's Mag. de Zool.*, 1818, p. 69.
† *Stettin. Ent. Zeitsch.*, 1845, p. 123.
‡ *Ann. Soc. Ent. France*, 1855, p. 51.

morsel of sugar. The beetle approached one of them, and tapped her several times on the head with her antennæ. The ant then opened her mandibles, and fed the Lomechusa as she would have done one of her own species. The Lomechusa crept on the sugar, but did not appear able to feed herself.

As might naturally be expected the myrmecophilous insects are not found indiscriminately in the nests of ants, but while some associate with several species, many are confined to a few or even to one.

V. Hagens is of opinion * that in some of these beetles which frequent the nests of two or more species of ant, varieties have been produced. Thus he has observed that the specimens of *Thiasophila angulata* in nests of *Formica pratensis* are darker than those found with *F. exsecta*. *Hetaerius sesquicornis* found with *Lasius niger* and *Tapinoma erraticum* are smaller than those which occur in the nests of larger ants; and the form of *Dinarda dentata*, which is met with in nests of *F. sanguinea*, has rather wider wing-cases than the normal type.[32]

I would by no means intend to imply that the relations between ants and the other insects which live with them are exhausted by the above suggestions. On the contrary, various other reasons may be imagined which may render the presence of these insects useful or agreeable to the ants. For instance, they may emit an odour which is pleasant to the ants. Again, Mr. Francis Galton has, I think, rendered it very probable that some of our domestic animals were kept as pets before they were made of any use. Unlikely as this may appear in some cases, for instance in the pig, we know as a fact that pigs are often kept by savages as pets. I would not put it forward as a suggestion which can be supported by any solid reasoning, but it seems not altogether impossible that some of these tame insects may be kept as pets.

It is from this point of view a very interesting fact

* *Berliner Ent. Zeitsch.*, 1865, p. 108.

that, according to Forel, in the cases of *Chennium* and *Batrisus* there is rarely more than one beetle in each nest.*

I now come to the relations existing between the different species of ants.

It is hardly necessary to say that, as a general rule, each species lives by itself.[33] There are, however, some interesting exceptions. The little *Stenamma westwoodi* is found exclusively in the nests of the much larger *F. rufa* and the allied *F. pratensis*. We do not know what the relations between the two species are. The *Stenamma*, however, follow the *Formica* when they change their nest, running about among them and between their legs, tapping them inquisitively with their antennæ, and even sometimes climbing on to their backs, as if for a ride, while the large ants seem to take little notice of them. They almost seem to be the dogs, or perhaps the cats, of the ants. Another small species, *Solenopsis fugax*, which makes its chambers and galleries in the walls of the nests of larger species, is the bitter enemy of its hosts. The latter cannot get at them, because they are too large to enter the galleries. The little *Solenopsis*, therefore, are quite safe, and, as it appears, make incursions into the nurseries of the larger ant, and carry off the larvæ as food. It is as if we had small dwarfs, about eighteen inches to two feet long, harbouring in the walls of our houses, and every now and then carrying off some of our children into their horrid dens.

Most ants, indeed, will carry off the larvæ and pupæ of others if they get a chance; and this explains, or at any rate throws some light upon, that most remarkable phenomenon, the existence of slavery among ants. If you place a number of larvæ and pupæ in front of a nest of the Horse ant (*F. rufa*), for instance, they are soon carried off; and those which are not immediately required for food remain alive for some time, and are even fed by their captors.

* *Fourmis de la Suisse*, p. 426.

Both the Horse ant (*Formica rufa*) and the slave ant (*F. fusca*) are abundant species, and it must not unfrequently occur that the former, being pressed for food, attack the latter and carry off some of their larvæ and pupæ. Under these circumstances it no doubt occasionally happens that the pupæ come to maturity in the nests of the Horse ant, and it is said that nests are sometimes, though rarely, found in which, with the legitimate owners, there are a few *F. fusca*. With the Horse ant this is, however, a very rare and exceptional phenomenon ; but with an allied species, *F. sanguinea*, a species which exists in some of our southern counties and throughout Europe, it has become an established habit. The *F. sanguinea* make periodical expeditions, attack neighbouring nests, carrying off the larvæ and pupæ, selecting those which will produce workers. When the latter come to maturity they find themselves in a nest consisting partly of *F. sanguinea*, partly of their own species, the results of previous expeditions. They adapt themselves to circumstances, assist in the ordinary household duties, and, having no young of their own species, feed and tend those of the *F. sanguinea*. But though the *F. sanguinea* are thus aided by their slaves, or as they should rather perhaps be called, their auxiliaries, they have not themselves lost the instinct of working. It seems not improbable that there is some division of functions between the two species, but we have as yet no distinct knowledge on this point ; and at any rate the *F. sanguinea* can " do " for themselves, and carry on a nest, if necessary, without slaves.[34]

The species usually enslaved by *F. sanguinea* are *Formica fusca* and *F. rufibarbis*, which indeed are so similar that they are perhaps varieties rather than species. Sometimes both occur in the same nest. André says that they also make slaves of *Formica gagates*.*

* *Rev. et Mag. de Zool.*, 1874, p. 164.

Schenk asserts * the same of *Lasius alienus*, and F. Smith of *L. flavus*, but Forel denies these statements.†

Another species, *Polyergus rufescens*, is much more dependent on its slaves, being, indeed, almost entirely so.

For the knowledge of the existence of slavery among ants we are indebted to Huber,‡ and I cannot resist quoting the passage in which he records his discovery: "On 17th June, 1804," he says, "while walking in the environs of Geneva, between four and five in the evening, I observed close at my feet, traversing the road, a legion of Rufescent ants.

"They moved in a body with considerable rapidity, and occupied a space of from eight to ten inches in length, by three or four in breadth. In a few minutes they quitted the road, passed a thick hedge, and entered a pasture ground, where I followed them. They wound along the grass without straggling, and their column remained unbroken, notwithstanding the obstacles they had to surmount. At length they approached a nest, inhabited by dark ash-coloured ants, the dome of which rose above the grass, at a distance of twenty feet from the hedge. Some of its inhabitants were guarding the entrance; but, on the discovery of an approaching army, darted forth upon the advanced guard. The alarm spread at the same moment in the interior, and their companions came forth in numbers from their underground residence. The Rufescent ants, the bulk of whose army lay only at the distance of two paces, quickened their march to arrive at the foot of the ant-hill; the whole battalion, in an instant, fell upon and overthrew the ash-coloured ants, who, after a short but obstinate conflict, retired to the bottom of their nest. The Rufescent ants now ascended the hillock, collected in crowds on the summit, and took possession of the principal avenues, leaving some of their companions to work an opening in the side of the

* *Cat. of Brit. Foss. Hymen.*, p. 7.

† *Fourmis de la Suisse*, p. 363.

‡ *The Natural History of Ants*, by M. P. Huber, p. 249.

ant-hill with their teeth. Success crowned their enterprise, and by the newly-made breach the remainder of the army entered. Their sojourn was, however, of short duration, for in three or four minutes they returned by the same apertures which gave them entrance, each bearing off in its mouth a larva or a pupa."

The expeditions generally start in the afternoon, and are from 100 to 2,000 strong.

Polyergus rufescens present a striking lesson of the degrading tendency of slavery, for these ants have become entirely dependent on their slaves. Even their bodily structure has undergone a change: the mandibles have lost their teeth, and have become mere nippers, deadly weapons indeed, but useless except in war. They have lost the greater part of their instincts: their art, that is, the power of building; their domestic habits, for they show no care for their own young, all this being done by the slaves; their industry—they take no part in providing the daily supplies; if the colony changes the situation of its nest, the masters are all carried by the slaves on their backs to the new one; nay, they have even lost the habit of feeding. Huber placed thirty of them with some larvæ and pupæ and a supply of honey in a box. "At first," he says, "they appeared to pay some little attention to the larvæ, they carried them here and there, but presently replaced them. More than one-half of the Amazons died of hunger in less than two days. They had not even traced out a dwelling, and the few ants still in existence were languid and without strength. I commiserated their condition, and gave them one of their black companions. This individual, unassisted, established order, formed a chamber in the earth, gathered together the larvæ, extricated several young ants that were ready to quit the condition of pupæ, and preserved the life of the remaining Amazons."

This observation has been fully confirmed by other naturalists. However small the prison, however large the quantity of food, these stupid creatures will starve in the midst of plenty rather than feed themselves.

M. Forel was kind enough to send me a nest of *Polyergus*, and I kept it under observation for more than four years. My specimens of *Polyergus* certainly never fed themselves, and when the community changed its nest, which they did several times, the mistresses were carried from the one to the other by the slaves. I was even able to observe one of their marauding expeditions, in which, however, the slaves took a part.

I do not doubt that, as Huber tells us, specimens of *Polyergus* if kept by themselves in a box would soon die of starvation, even if supplied with food. I have, however, kept isolated specimens for three months by giving them a slave for an hour or two a day to clean and feed them: under these circumstances they remained in perfect health, while, but for the slaves, they would have perished in two or three days. Excepting the slave-making ants, and some of the Myrmecophilous beetles above described, I know no case in nature of an animal having lost the instinct of feeding.

In *P. rufescens*, the so-called workers, though thus helpless and idle, are numerous, energetic, and in some respects even brilliant. In another slave-making ant, *Strongylognathus*, the workers are much less numerous, and so weak that it is an unsolved problem how they contrive to make slaves. In the genus *Strongylognathus* there are two species,[35] *S. huberi* and *S. testaceus*. *S. huberi*, which was discovered by Forel, very much resembles *Polyergus rufescens* in habits. They have sabre-like mandibles, like those of *Polyergus*, and their mode of fighting is similar, but they are much weaker insects; they make slaves of *Tetramorium cæspitum*, which they carry off as pupæ. In attacking the *Tetramorium* they seize them by the head with their jaws just in the same way as *Polyergus*, but have not strength enough to pierce them as the latter do. Nevertheless, the *Tetramorium* seem much afraid of them.

The other species, *Strongylognathus testaceus*, is even weaker than *S. huberi*, and their mode of life is still in many respects an enigma. They also keep the workers of *Tetramorium* in, so to say, a state of slavery, but how they procure the slaves is still a mystery.[36] They fight in the same manner as *Polyergus*: but yet Schenk, Von Hagens, and Forel all agree that they are no match for the *Tetramorium*, a courageous species, and one which lives in large communities. On one occasion Forel brought a nest of *Tetramorium* and put it down very near one of *Strongylognathus testaceus* with *Tetramorium* slaves. A battle at once commenced between the two communities. The *Strongylognathus* rushed boldly to the fight, but, though their side won the day, this was mainly due to the slaves. The *Strongylognathus* themselves were almost all killed; and though the energy of their attack seemed at first to disconcert their opponents, Forel assures us that they did not succeed in killing even a single *Tetramorium*. In fact, as Forel graphically observes, *Strongylognathus* is "une triste caricature" of *Polyergus*, and it seems almost impossible that by themselves they could successfully attack a nest of *Tetramorium*. Moreover, in *Strongylognathus*, the workers are comparatively few. Nevertheless, they are always found with the *Tetramorium*, and in these mixed nests there are no males or females of *Tetramorium*, but only those of *Strongylognathus*. Again, the whole work of the nest is done by the slaves, though *Strongylognathus* has not, like *Polyergus*, entirely lost the power of feeding itself.

But if the economy of *Strongylognathus* is an enigma, that of *Anergates* is still more mysterious.

The genus *Anergates* was discovered by Schenk,* who found a small community consisting of males, females, and workers, which he naturally supposed to belong to one species. Mayr, however, pointed out †

* "Die Nassauischen Ameisen-Species," *Stettin Ent. Zeit.*, 1853, p. 186.

† *Europ. Formicidæ*, p. 56.

that the workers were in fact workers of *Tetramorium cæspitum*; and it would appear that while in *Strongylognathus* the workers are comparatively few, *Anergates* differs from other ants in having no workers at all. The males and females live with *Tetramorium cæspitum*, and are in several respects very peculiar—for instance, the male is wingless. One might consider it rather a case of parasitism than of slavery, but the difficulty is that in these mixed nests there are no males, females, or young of *Tetramorium*. As to this all observers are agreed. It seems quite clear that *Anergates* cannot procure its slaves, if such they are, by marauding expeditions like those of *Polyergus*; in the first place, because the *Anergates* are too few, and secondly, because they are too weak. The whole question is rendered still more difficult by the fact that neither Von Hagens * nor Forel ever found either larvæ or pupæ of *Tetramorium* in the mixed nests. The community consisted of males and females of *Anergates*, accompanied and tended by workers of *Tetramorium cæspitum*. The *Anergates* are absolutely dependent upon their slaves, and cannot even feed themselves. The whole problem is, therefore, most puzzling and interesting.† [37]

As regards *Strongylognathus*, Von Hagens made two suggestions, the first being that this insect is really a monstrous form of *Tetramorium*. This, however, cannot at any rate be the case with *Anergates*. On the whole, then, he inclined to think that perhaps the nests containing *Strongylognathus* or *Anergates* are only parts of a community, and that the young of the *Tetramorium* are in another nest of the same community. This would account for the absence of the young of the *Tetramorium*, but would not remove all the difficulties. It is in other respects not consistent with what we know of the habits

* *Verh. des Natur. Vereines der Preuss. Rheinlande und Westphalens*, 1867, p. 53. See also V. Hagens, *Berl. Ent. Zeit.*, 1867, p. 102.

† On the contrary, in *Harpagoxenus sublævis*, a Finland species which lives in the nests of *Leptothorax muscorum* and *L. acervorum*, the workers only are known. The male, like that of *Anergates*, is wingless.

of ants, and on the whole I agree with Forel in thinking the suggestion untenable.

The difficulty of accounting for the numbers of *Tetramorium*, coupled with the absence of young, was indeed almost insuperable as long as the workers were supposed to live only for one year. My observations, however, which show that even in captivity workers may live for as long as six years, place the question in a different position, and give us, I think, a clue.

On the whole, I would venture to suggest that the male and female *Anergates* make their way into a nest of *Tetramorium*, and in some manner contrive to assassinate their queen. I have shown that a nest of ants may continue, even in captivity, for six years, without a queen. If, therefore, the female of *Anergates* could by violence or poison destroy the queen of the *Tetramorium*, we should in the following year have a community composed of two *Anergates*, their young, and workers of *Tetramorium*, in the manner described by Von Hagens and Forel. This would naturally not have suggested itself to these naturalists, because if the life of an ant had, as was formerly supposed, been confined to a single season, it would of course have been out of the question; but as we now know that the life of ants is so much more prolonged than had been supposed, it is at least not an impossibility.

It is conceivable that the *Tetramorium* may have gradually become harder and stronger; the marauding expeditions would then be less fruitful and more dangerous, and might become less and less frequent. If, then, we suppose that the females found it possible to establish themselves in nests of *Tetramorium*, the present state of things would almost inevitably be, by degrees, established. Thus we may explain the remarkable condition of *Strongylognathus*, armed with weapons which it is too weak to use, and endowed with instincts which it cannot exercise.

At any rate, these four genera offer us every gradation from lawless violence to contemptible parasitism. *Formica sanguinea,* which may be assumed to have comparatively recently taken to slave-making, has not as yet been materially affected.

Polyergus, on the contrary, already illustrates the lowering tendency of slavery. They have lost their knowledge of art, their natural affection for their young, and even their instinct of feeding! They are, however, bold and powerful marauders.

In *Strongylognathus,* the enervating influence of slavery has gone further, and told even on the bodily strength. They are no longer able to capture their slaves in fair and open warfare. Still they retain a semblance of authority, and, when roused, will fight bravely, though in vain.

In *Anergates,* finally, we come to the last scene of this sad history. We may safely conclude that in distant times their ancestors lived, as so many ants do now, partly by hunting, partly on honey; that by degrees they became bold marauders, and gradually took to keeping slaves; that for a time they maintained their strength and agility, though losing by degrees their real independence, their arts, and even many of their instincts; that gradually even their bodily force dwindled away under the enervating influence to which they had subjected themselves, until they sank to their present degraded condition—weak in body and mind, few in numbers, and apparently nearly extinct, the miserable representatives of far superior ancestors, maintaining a precarious existence as contemptible parasites of their former slaves.

Lespès has given a short but interesting account of some experiments made by him on the relations existing between ants and their domestic animals, from which it might be inferred that even within the limits of a single species some communities are more advanced than others. He states that specimens of the curious blind beetle *Claviger,* which always occurs with ants, when transferred from a nest of *Lasius niger* to another which kept none of these domestic beetles, were invariably attacked and eaten. From this he infers that the intelligence necessary to keep Clavigers is not coextensive with the species, but belongs only to certain communities and races, which, so to say, are more advanced in civilization than the rest of the species.

With reference to the statements of Lespès, I have more than once transferred specimens of *Platyarthrus* from one nest to another, and always found them received amicably. I even placed specimens from a nest of *Lasius flavus* in one of *Formica fusca* with the same result. I brought from the South of France some specimens of a different species, as yet undescribed, and put them in a nest of *Formica fusca*, where they lived for some time, and brought up more than one brood of young. These creatures, however, occur in most ants' nests, while Clavigers are only found in some.

But whether there are differences in advancement within the limits of the same species or not, there are certainly considerable differences between the different species, and one may almost fancy that we can trace stages corresponding to the principal steps in the history of human development.

I do not now refer to slave-making ants, which represent an abnormal, or perhaps only a temporary state of things, for slavery seems to tend in ants as in men to the degradation of those by whom it is adopted, and it is not impossible that the slave-making species will eventually find themselves unable to compete with those which are more self-dependent, and have reached a higher phase of civilization. But putting these slave-making ants on one side, we find in the different species of ants different conditions of life, curiously answering to the earlier stages of human progress. For instance, some species, such as *Formica fusca*, live principally on the produce of the chase; for though they feed partly on the honey-dew of aphides, they have not domesticated these insects.

These ants probably retain the habits once common to all ants. They resemble the lower races of men, who subsist mainly by hunting. Like them they frequent woods and wilds, live in comparatively small communities, and the instincts of collective action are but little developed among them. They hunt singly, and their battles are single combats, like those of the Homeric heroes. Such species as *Lasius flavus* represent a distinctly higher type of social life; they show more skill in architecture, may literally be said to have domesticated certain species of aphides, and may be compared to the pastoral stage of human progress—to the races which live on the produce of their flocks and herds. Their communities are more numerous; they act much more in concert; their battles are not mere single combats, but they know how to act in combination. I am disposed to hazard the conjecture that they will gradually exterminate the mere hunting species, just as savages disappear before more advanced races. Lastly, the agricultural nations may be compared with the harvesting ants.

Thus there seem to be three principal types, offering a curious analogy to the three great phases—the hunting, pastoral, and agricultural stages—in the history of human development.[38]

CHAPTER V

BEHAVIOUR TO RELATIONS

Mr Grote, in his *Fragments on Ethical Subjects,* regards it as an evident necessity that no society can exist without the sentiment of morality. "Everyone," he says, "who has either spoken or written on the subject, has agreed in considering this sentiment as absolutely indispensable to the very existence of society. Without the diffusion of a certain measure of this feeling throughout all the members of the social union, the caprices, the desires, and the passions of each separate individual would render the maintenance of any established communion impossible. Positive morality, under some form or other, has existed in every society of which the world has ever had experience."

If this be so, the question naturally arises whether ants also are moral and accountable beings. They have their desires, their passions, even their caprices. The young are absolutely helpless. Their communities are sometimes so numerous, that perhaps London and Pekin are almost the only human cities which can compare with them. Moreover, their nests are no mere collections of independent individuals, nor even temporary associations like the flocks of migratory birds; but organized communities labouring with the utmost harmony for the common good. The remarkable analogies which, in so many ways, they present to our human societies, render them peculiarly interesting to us, and one cannot but long to know more of their character, how the world appears to them, and to what extent they are conscious and reasonable beings.

For my own part I cannot make use of Mr Grote's argument, because I have elsewhere * attempted to show that, even as regards man, the case is not by any means clear. But however this may be, various observers have recorded in the case of ants instances of attachment and affection.

Forel lays it down as a general rule that if ants are slightly injured, or rather unwell, their companions take care of them: on the other hand, if they are badly wounded or seriously ill, they are carried away from the nest, and left to perish.[39]

Latreille, also, makes the following statement: "Le sens de l'odorat," he says,† "se manifestant d'une manière aussi sensible, je voulois profiter de cette remarque pour en découvrir le siége. On a soupçonné depuis longtemps qu'il résidoit dans les antennes. Je les arrachai à plusieurs fourmis fauves ouvrières, auprès du nid desquelles je me trouvois. Je vis aussitôt ces petits animaux que j'avois ainsi mutilés tomber dans un état d'ivresse ou une espèce de folie. Ils erroient çà et là, et ne reconnoissoient plus leur chemin. Ils m'occupoient; mais je n'étais pas le seul. Quelques autres fourmis s'approchèrent de ces pauvres affligées, portèrent leur langue sur leurs blessures, et y laissèrent tomber une goutte de liqueur. Cet acte de sensibilité se renouvela plusieurs fois; je l'observois avec une loupe. Animaux compatissans! quelle leçon ne donnez-vous pas aux hommes."

"Jamais," says M. de Saint Fargeau,‡ "une Fourmi n'en rencontre une de son espèce blessée, sans l'enlever et la transporter à la fourmilière. L'y soigne-t-elle? Je ne sais, mais je vois dans ce fait une bienveillance que je ne retrouve dans aucun autre insecte, même social."

I have not felt disposed to repeat M. Latreille's experiment, and M. de St Fargeau's statement is I

* *The Origin of Civilization and the Primitive Condition of Man.*

† *Hist. Nat. des Fourmis*, p. 41.

‡ *Hist. Nat. des Ins. Hyménoptères*, vol. i, p. 99.

think by no means correct; indeed, many of my experiences seem to show not only a difference of character in the different species of ants, but that even within the limits of the same species there are individual differences between ants, just as between men.

I will commence with the less favourable aspect.

On one occasion (13th August) a worker of *Lasius niger*, belonging to one of my nests, had got severely wounded, but not so much so that she could not feed; for though she had lost five of her tarsi, finding herself near some syrup, she crept to it and began to feed. I laid her gently on her back close to the entrance into the nest. Soon an ant came up to the poor sufferer, crossed antennæ with her for a moment, then went quietly on to the syrup and began to feed. Afterwards three other ants did the same; but none took any more notice of her.

15th August.—I found at 1 p.m. a *Myrmica ruginodis* which, probably in a fight with another ant, had lost the terminal portion of both her antennæ. She seemed to have lost her wits. I put her into her nest; but the others took no notice of her; and after wandering about a little she retired into a solitary place where she remained from 3 p.m. to 8 p.m. without moving. The following morning I looked for her at 5.30, and found her still at the same spot. She remained there till 9, when she came out. She remained out all day; and the following morning I found her dead.

Indeed, I have often been surprised that in certain cases ants render one another so little assistance. The tenacity with which they retain their hold on an enemy they have once seized is well known. M. Mocquerys even assures us that the Indians of Brazil made use of this quality in the case of wounds; causing an ant to bite the two lips of the cut and thus bring them together, after which they snip off the ant's head, which thus holds the lips together. He asserts that he has often seen natives with wounds in course of healing with the assistance of seven or eight ants' heads! * Now I have often observed that some of my ants had the heads of others hanging on to their legs for a considerable time; and as this must certainly be very inconvenient, it seems remarkable that their friends should not relieve them of such an awkward encumbrance.

The behaviour of ants to one another differs also much according to circumstances; whether, for instance, they are alone, or supported by friends. An ant which would run away in the first case will defend herself bravely in the second.

If an ant is fighting with one of another species, her friends rarely come to her assistance. They seem generally (unless a regular battle is taking place) to take no interest in the matter, and do not even stop to look on. Some species, indeed, in such cases never appear to help one another; and even when the reverse is the case, as for instance in the genus *Lasius*, the truth seems to be that several of them attack the same enemy—their object being to destroy the foe, rather than to save their friend.

On one occasion several specimens of *Formica fusca* belonging to one of my nests were feeding on some honey spread on a slip of glass (22nd May). One of them had got thoroughly entangled in it. I took her and put her down just in front of another specimen belonging to the same nest, and close by I placed a drop of honey. The ant devoted herself to the honey and entirely neglected her friend, whom she left to perish. Again, some specimens of *Cremastogaster scutellaris* were feeding quietly (22nd May) on some honey spread on a slip of glass, and one of them had got thoroughly mixed in it. I took her out and put her on the glass close by. She could not disentangle herself; not one of her friends took the least notice of her, and eventually she died. I then chloroformed one, and put her on the board among her friends. Several

* *Ann. Soc. Ent. France*, 2 sér. tom. ii, p. 67.

touched her, but from 12 to 2.30 p.m. none took any particular notice of her.

On the other hand, I have only on one occasion seen a living ant expelled from her nest. This happened in a community of *F. fusca.* I observed (23rd April, 1880) an ant carrying another belonging to the same community away from the nest. The condemned ant made a very feeble resistance. The first ant carried her burthen hither and thither for some time, evidently trying to get away from the nest, which was enclosed in the usual manner by a fur barrier. After watching for some time I provided the ant with a paper bridge, up which she immediately went, dropped her victim on the far side, and returned home. Could this have been a case in which an aged or invalid ant was being expelled from the nest ?

I have often had ants in my nests to which mites had attached themselves.

Thus, on 14th October, 1876, I observed that one of my ants (*Formica fusca*) had a mite attached to the underside of her head, which it almost equalled in size. The poor ant could not remove it herself, and, being a queen, never left the nest, so that I had no opportunity of doing so. For more than three months none of her companions performed this kind office for her.

With reference to this part of the subject, also, I have made some experiments.

3rd January, 1876.—I immersed an ant (*Lasius niger*) in water for half an hour ; and when she was then to all appearance drowned, I put her on a strip of paper leading from one of my nests to some food. The strip was half an inch wide ; and one of my marked ants belonging to the same nest was passing continually to and fro over it to some food. The immersed ant lay there an hour before she recovered herself ; and during this time the marked ant passed by eighteen times without taking the slightest notice of her.

I then immersed another ant in the water for an hour, after which I placed her on the strip of paper as in the preceding case. She was three-quarters of an hour before she recovered: during this time two marked ants were passing to and fro; one of them went by eighteen times and the other twenty times; and two other ants also went over the paper; but none of them took the slightest notice of their drowned friend.

I then immersed another ant for an hour, and put her on the strip of paper. She took an hour to recover. The same two marked ants as in the previous observation were at work. One passed thirty times, the other twenty-eight times, besides which five others passed by; but not one took the slightest notice.

I immersed three ants for eight hours, and then put them on the strip of paper. They began to recover in three-quarters of an hour, but were not quite themselves till half an hour afterwards. During the first three-quarters of an hour two marked ants passed, each four times; and two others also went by. During the following half hour the two marked ants passed sixteen times, and three others; but none of them took any notice.

I immersed another ant for forty minutes, and put her on the strip of paper. She recovered in twenty minutes, during which time the marked ones, which were the same as in the preceding case, went by fourteen times without taking any notice.

I immersed two ants for ten hours, and then placed them on the strip of paper. The same two marked ants passed respectively eighteen and twenty-six times, and one other passed by also without taking any notice. After this I left off watching.

I immersed two ants for four hours, and then put them on the strip of paper. They began to recover in an hour, during which two marked ants, not the same as in the preceding case, passed respectively twenty-eight and ten times, and two others went by; but none of them took any notice.

I immersed an ant for an hour, and then put her on the same strip of paper as in the previous cases. A marked ant passed her twelve times; three others also went by but took no notice of her; but, on the other hand, a fourth picked her up and carried her off into the nest.

Again, I immersed an ant for an hour, and put her on the strip of paper. The marked ant passed twice, after which she did not return. Soon after, another ant came by and, picking up the immersed one, carried her off to the nest.

I do not bring forward these cases as proof or even as evidence that ants are less tender to friends in distress than previous observers have stated to be the case; but they certainly show that tenderness is not invariably the rule; and, especially when taken in connection with the following cases, they are interesting illustrations of the individual differences existing between ants—that there are Priests and Levites and good Samaritans. among them, as among men.

As evidence both of their intelligence and of their affection for their friends, it has been said by various observers that when ants have been accidentally buried they have been very soon dug out and rescued by their companions. Without for one moment doubting the facts as stated, we must remember the habit which ants have of burrowing in loose fresh soil, and especially their practice of digging out fresh galleries when their nests are disturbed.

It seemed to me, however, that it would not be difficult to test whether the excavations made by ants under the circumstances were the result of this general habit, or really due to a desire to extricate their friends.

With this view I tried the following experiments:

(1) On 20th August I placed some honey near a nest of *Lasius niger* on a glass surrounded with water, and so arranged that in reaching it the ants passed over another glass covered with a layer of sifted earth, about one-third of an inch in thickness. I then put some ants to the honey, and by degrees a considerable number

collected round it. Then at 1.30 p.m. I buried an ant from the same nest under the earth, and left her there till 5 p.m., when I uncovered her. She was only just covered by the earth, and was none the worse, but during the whole time not one of her friends had taken the least notice of her.

(2) I arranged (1st September) some honey again in the same way. At 5 p.m. about fifty ants were at the honey, and a considerable number passing to and fro. I then buried an ant as before, taking of course one from the same nest. At 7 p.m. the number of ants at the honey had nearly doubled. At 10 p.m. they were still more numerous, and had carried off about two-thirds of the honey. At 7 a.m. the next morning the honey was all gone, two or three were still wandering about, but no notice had been taken of the prisoner, whom I then let out. In this case I allowed the honey to be finished, because I thought it might perhaps be alleged that the excitement produced by such a treasure distracted their attention, or even (on the principle of doing the greatest good to the greatest number) that they were intelligently wise in securing a treasure of food before they rescued their comrade, who, though in confinement, was neither in pain nor danger. So far as the above ants, however, are concerned, this cannot, I think, be urged.

(3) On the 8th September I repeated the experiment, burying some ants at 4 p.m. Up to 6.3 no attempt had been made to release them. I let them out and buried some more. The next morning, at 7 a.m., the honey was all gone, some ants were still wandering about, but no notice had been taken of the captives, whom I then liberated.

(4) I then (21st August) made exactly the same experiment with *Myrmica ruginodis*, as representing the other great family of ants, and with the same result.

In order to test the affection of ants belonging to the same nest for one another I tried the following experiments. I took six ants from a nest of *F. fusca*, imprisoned them in a small bottle, one end of which was covered with a layer of muslin. I then put the muslin close to the door of the nest. The muslin was of open texture, the meshes, however, being sufficiently small to prevent the ants from escaping. They could not only, however, see one another, but communicate freely with their antennæ. We now watched to see whether the prisoners would be tended or fed by their friends. We could not, however, observe that the least notice was taken of them. The experiment, nevertheless, was less conclusive than could be wished, because they might have been fed at night, or at some time when we were not looking. It struck me, therefore, that it would be interesting to treat some strangers also in the same manner.

On 2nd September, therefore, I put two ants from one of my nests of *F. fusca* into a bottle, the end of which was tied up with muslin as described, and laid it down close to the nest. In a second bottle I put two ants from another nest of the same species. The ants which were at liberty took no notice of the bottle containing their imprisoned friends. The strangers in the other bottle, on the contrary, excited them considerably. The whole day one, two, or more ants stood sentry, as it were, over the bottle. In the evening no less than twelve were collected round it, a larger number than usually came out of the nest at any one time. The whole of the next two days, in the same way, there were more or less ants round the bottle containing the strangers; while, as far as we could see, no notice whatever was taken of the friends. On the 9th the ants had eaten through the muslin, and effected an entrance. We did not chance to be on the spot at the moment; but as I found two ants lying dead, one in the bottle and one just outside, I think there can be no doubt that the strangers were put to death. The friends throughout were quite neglected.

21st September.—I then repeated the experiment, putting three ants from another nest in a bottle as before. The same scene was repeated. The friends were neglected. On the other hand, some of the ants were always watching over the bottle containing the strangers, and biting at the muslin which protected them. The next morning at 6 a.m. I found five ants thus occupied. One had caught hold of the leg of one of the strangers, which had unwarily been allowed to protrude through the meshes of the muslin. They worked and watched, though not, as far as I could see, with any system, till 7.30 in the evening, when they effected an entrance, and immediately attacked the strangers.

24th September.—I repeated the same experiment with the same nest. Again the ants came and sat over the bottle containing the strangers, while no notice was taken of the friends.

The next morning again, when I got up, I found five ants round the bottle containing the strangers, none near the friends. As in the former case, one of the ants had seized a stranger by the leg, and was trying to drag her through the muslin. All day the ants clustered round the bottle, and bit perseveringly, though not systematically, at the muslin. The same thing happened all the following day.

These observations seemed to me sufficiently to test the behaviour of the ants belonging to this nest under these circumstances. I thought it desirable, however, to try also other communities. I selected, therefore, two other nests. One was a community of *Polyergus rufescens* with numerous slaves. Close to where the ants of this nest came to feed, I placed as before two small bottles, closed in the same way—one containing two slave ants from the nest, the other two strangers. These ants, however, behaved quite unlike the preceding, for they took no notice of either bottle, and showed no sign either of affection or hatred. One is almost tempted to surmise that the warlike spirit of these ants was broken by slavery.

The other nest which I tried, also a community of *Formica fusca*, behaved exactly like the first. They took no notice of the bottle containing the friends, but clustered round and eventually forced their way into that containing the strangers.

It seems, therefore, that in these curious insects hatred is a stronger passion than affection.

Some of those who have done me the honour of noticing my papers in the *Linnean Journal*, have assumed that I disputed altogether the kindly feelings which have been attributed to ants. I should, however, be very sorry to treat my favourites so unfairly. So far as I can observe, ants of the same nest never quarrel. I have never seen the slightest evidence of ill-temper in any of my nests: all is harmony. Nor are instances of active assistance at all rare. Indeed, I have myself witnessed various cases showing care and tenderness on their part.

In one of my nests of *Formica fusca* was an ant which had come into the world without antennæ. Never having previously met with such a case, I watched her with great interest; but she never appeared to leave the nest. At length one day I found her wandering about in an aimless sort of manner, and apparently not knowing her way at all. After a while she fell in with some specimens of *Lasius flavus*, who directly attacked her. I at once set myself to separate them; but whether owing to the wounds she had received from her enemies, or to my rough, though well-meant handling, or to both, she was evidently much wounded, and lay helplessly on the ground. After some time another *Formica fusca* from her nest came by. She examined the poor sufferer carefully, then picked her up carefully and carried her away into the nest. It would have been difficult for any one who witnessed this scene to have denied to this ant the possession of humane feelings.

Again, in one of my nests of *Formica fusca* on 23rd

PLATE II

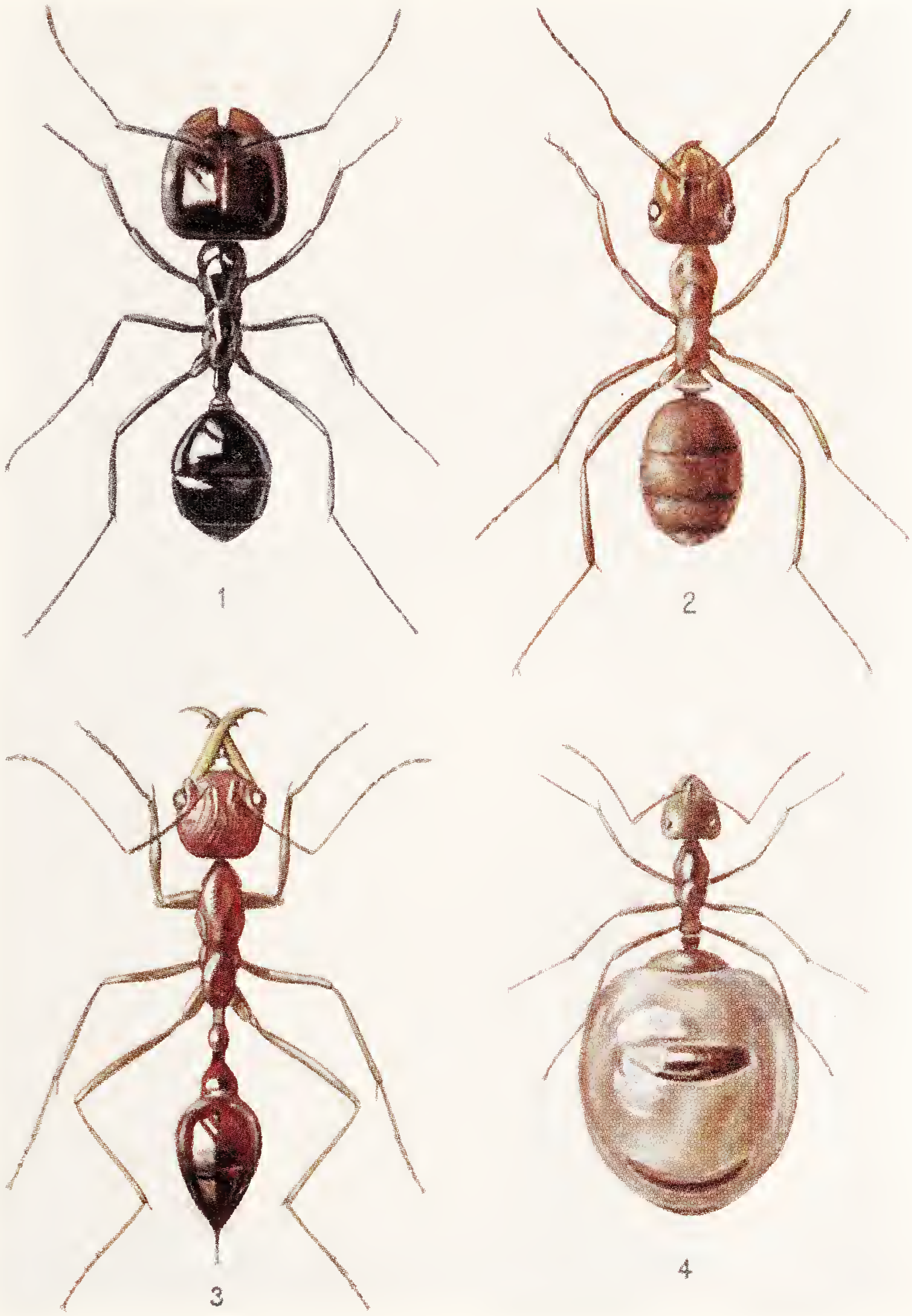


Fig. 1. *Messor barbarus*, large worker. A Mediterranean harvesting ant ($\times 3\frac{1}{2}$)

,, 2. *Formica rufa*, worker. The horse or wood ant ($\times 6$)

,, 3. *Myrmecia gulosa*, worker. An Australian bull-dog ant ($\times 2$)

,, 4. *Myrmecocystus melliger*, worker (replete). A North American honey-ant ($\times 2\frac{1}{2}$)

[*face p.* 80

January, 1881, I perceived a poor ant lying on her back and quite unable to move. The legs were in cramped attitudes, and the two antennæ rolled up in spirals. She was, of course, altogether unable to feed herself. After this I kept my eye on her. Several times I tried uncovering the part of the nest where she was. The other ants soon carried her into the shaded part. On 4th March the ants were all out of the nest, probably for fresh air, and had collected together in a corner of the box; they had not, however, forgotten her, but had carried her with them. I took off the glass lid of the box, and after a while they returned as usual to the nest, taking her in again. On 5th March she was still alive, but on the 15th, notwithstanding all their care, she was dead!

At the present time I have two other ants perfectly crippled in a similar manner, and quite unable to move, which had lived in two different nests, belonging also to *F. fusca*, the one for five the other for four months.

In May, 1879, I gave a lecture on Ants at the Royal Institution, and was anxious to exhibit a nest of *Lasius flavus* with the queen. While preparing the nest, on 9th May, we accidentally crushed the queen. The ants, however, did not desert her, or drag her out as they do dead workers, but, on the contrary, carried her with them into the new nest, and subsequently into a larger one with which I supplied them, congregating round her, just as if she had been alive, for more than six weeks, when we lost sight of her.

In order to ascertain whether ants knew their fellows by any sign or pass word, as had been suggested in the case of bees, I was anxious to see if they could recognize them when in a state of insensibility. I tried therefore the following experiments with some specimens of *Lasius flavus*.

On 10th September, at 6 p.m., a number of these ants were out feeding on some honey, placed on one of my tables and surrounded by a moat of water. I chloroformed four of them and also four from a nest in my park, at some distance from the place where the first had been originally procured, painted them, and put them close to the honey. Up to 8.20 the ants had taken no notice of their insensible fellow creatures. At 9.20 I found that four friends were still lying as before, while the four strangers had been removed. Two of them I found had been thrown over the edge of the board on which the honey was placed. The other two I could not see.

Again, on 14th September, at 8.40, I put in the same way four friends marked white, and four strangers marked red, close to where my *L. flavus* were out feeding on honey placed on a slip of glass over water. For some hours they took no notice of them. At length one took a friend, and after carrying her about some time dropped her, at 12.40, into the water. Some time after another took up a stranger, and carried her into the nest at 2.35. A second stranger was similarly carried into the nest at 2.55, a third at 3.45, while the fourth was thrown over the edge of the board at 4.20. Shortly after this two of the strangers were brought out of the nest again and thrown into the water. A second friend was thrown away, like the first, at 4.58, the third at 5.17, and the fourth at 5.46. I could not ascertain what happened to the last stranger, but have little doubt that she was brought out of the nest and thrown away like the rest.

On the following day at 6.45 I tried the same experiment again, only reversing the colours by which they were distinguished. At 7 one of the strangers was carried off and dropped over the edge of the glass into the water, and at 8 a second. At 8.45 a friend was taken up and, after being carried about some time, was thrown into the moat. At 9.45 a friend was picked up and carried into the nest, but brought out again and thrown away about 3 in the afternoon. The other four remained where they were placed until 8 p.m., and though the other ants often came up and examined them, they did not carry them off.

29th September.—Again placed nine chloroformed ants, five friends and four strangers, close to where a number were feeding. There was a continual stream of ants to the honey, ten or fifteen being generally there at once.

A stranger	was picked	up at	10.20	and dropped into the water at	10.32
,,	,,	,,	10.22	,,	10.35
A friend	,,	,,	11.22	,,	11.42
A stranger	,,	,,	11.35	,,	11.50
,,	,,	,,	11.41	,,	11.45

Shortly after the others were picked up and carried away to the edge of the board, where they were dropped, but none were taken into the nest.

2nd October.—Again at 10 a.m. placed ten chloroformed ants, five friends and five strangers, close to where some were feeding. They were picked up and carried off as before in the following order :—

At 11.5	a stranger	was picked up and dropped at	11.15
11.12	a friend	,, ,,	11.50
11.25	a stranger	,, ,,	11.36
12.7	,,	,, ,,	12.45
12.10	a friend	,, ,,	12.16
1.10	a stranger	,, ,,	2.6
1.42	a friend	,, ,,	1.46
1.52	,,	,, ,,	1.56
2.6	,,	,, ,,	3.10

Only one of them, and that one a stranger, was carried into the nest at 12.45, but brought out again at 1.10.

6th October.—At 9 a.m. again tried the same experiment with four strangers and five friends.

At 9.25	a friend	was picked up and dropped at	9.31
9.32	,,	,, ,,	9.38
9.35	a stranger	,, ,,	9.45
9.45	,,	,, ,,	9.52
10.8	a stranger	,, ,,	10.17
10.17	a friend	,, ,,	10.20
10.22	a stranger	,, ,,	10.25
10.28	,,	,, ,,	10.40
10.25	a friend	,, ,,	10.31

None of them were carried into the nest.

These experiments seem to prove that under such circumstances ants, at least those belonging to this species, do not carry off their friends (when thus rendered insensible) into a place of safety.

I think, however, that in this experiment the ants being to all intents and purposes dead, we could not expect that any difference would be made between friends and strangers. I therefore repeated the same experiment, only, instead of chloroforming the ants, I intoxicated them. This experiment is more difficult, as it is not in all cases easy to hit off the requisite degree of intoxication. The numbers therefore of friends and strangers are not quite the same, because in some cases the ants recovered too quickly and had to be removed. In such cases I have latterly replaced the ant so removed by another, so as to keep the number of friends and strangers about equal. The sober ants seemed somewhat puzzled at finding their intoxicated fellow creatures in such a disgraceful condition, took them up, and carried them about for a time in a somewhat aimless manner.

20th November.—I experimented with six friends and six strangers, beginning at 11.

At 11.30 a friend was carried to the nest.

11.50 a stranger was dropped into the water.
12.30 ,, ,, ,,
12.31 a friend ,, ,,
1.10 a stranger ,, ,,
1.18 ,, ,, ,,
1.27 ,, ,, ,,
1.30 a friend (partly recovered) was taken to the nest.

2.30 a friend was taken up and carried about till 2.55; she was then taken to the nest, but at the door the bearer met two other ants, which seized the intoxicated one, carried her off, and eventually dropped her into the water.

At 3.35 a friend was carried to the nest.

Out of these twelve, five strangers and two friends were dropped into the water; none of the strangers, but three friends were taken to the nest. None of the friends were brought out of the nest again.

22nd November.—Experimented in the same way on four friends and four strangers, beginning at 12 o'clock.

At 12.16 a stranger was taken and dropped into the water.
12.21 ,, ,, ,,
12.23 ,, ,, ,,
12.40 ,, ,, ,,

I then put four more strangers treated as before.

At 3.10 a stranger was taken and dropped into the water.
3.30 ,, ,, ,,
3.35 ,, ,, ,,
3.44 a friend (partly recovered) was taken back to the nest.
4.10 a stranger was taken and dropped into the water.
4.13 a friend (partly recovered) was taken back to the nest.

In this case eight strangers were dropped into the water, and none were taken to the nest; two friends, on the contrary, were taken to the nest, and none were dropped into the water.

1st December.—Experimented with five friends and five strangers, beginning at 2.15.

At 2.30 a stranger was dropped into the water.
3.2 ,, ,, ,,
3.20 a friend was taken into the nest.
3.35 a stranger was taken into the nest, but afterwards brought out again and thrown into the water.
3.52 ,, ,, ,,
4. 5 I put out four more friends and as many strangers.

At 4.45 a stranger was dropped into the water.
5.10 ,, taken into the nest, but afterwards brought out and thrown into the water.
5.24 ,, taken into the nest, but afterwards brought out and thrown into the water.
5.55 a friend was thrown into the water.
6. 4 a stranger ,, ,,
6. 4 ,, ,, ,,
6. 8 a friend was taken into the nest.
6.20 ,, ,, ,,
6.23 ,, ,, ,,
6.30 a stranger was dropped into the water.
6.50 a friend ,, ,,
8. 5 a friend was taken into the nest.

In this case two friends were thrown into the water and seven taken into the nest; while six strangers were thrown into the water and four were taken into the nest; all of these, however, were afterwards brought out again and thrown away.

8th December.—Experimented with six friends and six strangers, beginning at 11.30.

At 11.30 a friend was carried to nest.
11.47 ,, ,,
11.50 ,, ,,
11.52 ,, ,,
11.56 a friend was dropped into water.
11.58 a stranger ,, ,,
11.58 ,, ,, ,,
12 a stranger was carried to nest.
12. 2 ,, ,,
12. 3 ,, ,,

I then put four more of each, and as a friend or a stranger was carried off, replaced her by another.

At 12.45 a friend to the water.
12.58 a stranger was dropped into the water.

At	1	a friend to the nest.
	1	,, ,,
	1	,, ,,
	1.58	,, ,,
	1.59	,, ,,
	2.30	a stranger to the water.
	2.30	,, ,,
	2.35	a stranger to the nest.
	2.42	a stranger to the water.
	2.48	,, ,,
	2.51	,, ,,
	2.52	,, ,,
	2.55	a friend to the nest.
	2.55	a stranger to the water.
	2.55	,, ,,
	3. 2	a friend to the water.
	3. 6	a stranger to the water.
	3.12	a friend to the water.
	3.15	,, ,,
	3.16	a friend to the nest.
	3.22	a stranger to the water.
	3.25	,, ,,
	3.25	a friend to the nest.
	3.35	a stranger to the water.
	3.50	a friend to the nest.
	3.50	,, ,,

All these ants appeared quite insensible. Altogether sixteen friends were taken to the nest and five thrown into the water, while of the strangers only three were taken to the nest, and fifteen were thrown into the water. Moreover, as in the preceding observation, even the three strangers which were at first taken to the nest were soon brought out again and thrown away; while this was not the case with any of the friends as far as we could ascertain, though we searched diligently for them also. In this case also all the intoxicated ants were motionless and apparently insensible.

15th January.—Repeated the same experiment, beginning at 12.20. Up to 7 p.m. not one of the intoxicated ants had been moved. At 8.20 we found a stranger in the water, at 9.30 another, and at the following morning a third. The others were untouched.

17th January.—Repeated the same experiment, beginning at 11.30.

At 12 a friend was carried to the nest.
12.20 a stranger was dropped into the water.
12.34 a friend was carried to the nest.
12.40 a stranger was dropped into the water.
12.45 a friend was carried to the nest.
1 a stranger ,, ,,
1 ,, ,, water.
(Stopped observing till 2.)
2.30 a stranger was dropped into the water.
2.30 a stranger was carried to the nest.
4.10 ,, ,, ,,
4.30 a friend ,, ,,
6.20 a stranger ,, water.
6.35 ,, ,, ,,

Thus, then, the general results were that the ants removed forty-one friends and fifty-two strangers. Of the friends, thirty-two were carried into the nest and nine were thrown into the water. Of the strangers, on the contrary, forty-three were thrown into the water; only nine were taken into the nest, and seven of these were shortly afterwards brought out again and thrown away. Indeed, I fully believe that the other two were treated in the same manner, though we could not satisfy ourselves of the fact. But it was only by very close observation that the seven were detected, and the other two may well have escaped notice.

It seems clear, therefore, that even in a condition of insensibility these ants were recognized by their friends.

Tabular View.—Experiments on Chloroformed and Intoxicated Ants.

CHLOROFORMED ANTS.

	Friends.			Strangers.		
	Carried to Nest.	To water.	Unremoved.	Carried to Nest.	To water.	Unremoved.
Sept. 10	—	—	4	—	4	—
„ 14	—	4	—	2 and brought out again.	2	—
„ 15	1 and brought out again.	1	—	—	2	2
„ 29	—	5	—	—	4	—
Oct. 2	—	5	—	1 and brought out again.	4	—
„ 6	—	5	—	—	4	—
	1	20	4	3	20	2

INTOXICATED ANTS.

Nov. 20	3	2	—	—	5	1
„ 22	2	—	2	—	8	—

In these cases some of the Ants had partly recovered; in the following they were quite insensible.

Dec. 1	7 none brought out again.	2	—	3 all these brought out again.	6	—
„ 8	16 none brought out again.	5	—	3 all these brought out again.	15	—
Jan. 15	—	—	4	—	3	1
„ 17	4 none bro't out again.	—	—	3 one brought out again.	6	—
	27	7	4	2	30	1

CHAPTER VI

RECOGNITION OF FRIENDS

It has been already shown that with ants, as with bees, while the utmost harmony reigns between those belonging to the same community, all others are enemies. I have already given ample proof that a strange ant in never tolerated in a community. This, of course, implies that all the bees or ants of a community have the power of recognizing one another, a most surprising fact, when we consider the shortness of their life and their immense numbers. It is calculated that in a single hive there may be as many as 50,000 bees, and in the case of ants the numbers are still greater. In the large communities of *Formica pratensis* it is probable that there may be as many as from 400,000 to 500,000 ants, and in other cases even these large numbers are exceeded.

If, however, a stranger is put among the ants of another nest, she is at once attacked. On this point I have satisfied myself, as will be seen in the following pages, that the statements of Huber and others are perfectly correct. If, for instance, I introduced a stranger into one of my nests, say of *Formica fusca* or *Lasius niger*, she was at once attacked. One ant would seize her by an antenna, another by a leg, and she was either dragged out of the nest or killed.

Moreover, we have not only to deal with the fact that ants know all their comrades, but that they recognize them even after a lengthened separation.

Huber mentions that some ants which he had kept in captivity having accidentally escaped, "met and recognized their former companions, fell to mutual caresses with their antennæ, took them up by their mandibles, and led them to their own nests; they came presently in a crowd to seek the fugitives under and about the artificial ant-hill, and even ventured to reach the bell-glass, where they effected a complete desertion by carrying away successively all the ants they found there. In a few days the ruche was depopulated. These ants had remained four months without any communication." * This interesting statement has been very naturally copied by succeeding writers. See, for instance, Kirby and Spence's *Introduction to Entomology*, vol. ii, p. 66, and Newport, *Trans. of the Entomological Society of London*, vol. ii, p. 239.

Forel, indeed, regards the movements observed by Huber as having indicated fear and surprise rather than affection; though he is quite disposed to believe, from his own observations, that ants would recognize one another after a separation of several months.

The observation recorded by Huber was made casually, and he did not take any steps to test it by subsequent experiments. The fact, however, is of so much importance that I determined to make further observations on the subject. In the first place, I may repeat that I have satisfied myself by many experiments, that ants from one community introduced into another—always be it understood of the same species—are attacked, and either driven out or killed. It follows, therefore, that as within the nest the most complete harmony prevails—indeed, I have never seen a quarrel between sister ants—they must by some means recognize one another.

When we consider their immense numbers this is sufficiently surprising; but that they should recognize one another, as stated by Huber, after a separation of months is still more astonishing.

I determined therefore to repeat and extend his observations.

Accordingly, on 20th August, 1875, I divided a colony

* Huber, p. 192.

of *Myrmica ruginodis*, so that one half were in one nest, A, and the other half in another, B, and were kept entirely apart.

On 3rd October, I put into nest B a stranger and an old companion from nest A. They were marked with a spot of colour. One of them immediately flew at the stranger; of the friend they took no notice.

18th October.—At 10 a.m. I put in a stranger and a friend from nest A. In the evening the former was killed, the latter was quite at home.

19th October.—I put one in a small bottle with a friend from nest A. They did not show any enmity. I then put in a stranger; and one of them immediately began to fight with her.

24th October.—I again put into the nest a stranger and a friend. The former was attacked, but not the latter. The following day I found the former almost dead, while the friend was all right.

31st October.—I again put a stranger and a friend into the nest. The former was at once attacked; in this case the friend also was, for a moment, seized by the leg, but at once released again. On the following morning the stranger was dead, the friend was all right.

7th November.—Again I put in a stranger and a friend. The former was soon attacked and eventually driven out; of the latter they did not seem to me to take any particular notice. I could see no signs of welcome, no gathering round a returned friend; but, on the other hand, she was not attacked.

Again, I separated one of my colonies of *Formica fusca* into two halves on 4th August, 1875, and kept them entirely apart. From time to time I put specimens from the one half back into the other. At first the friends were always amicably received, but after some months' separation they were occasionally attacked, as if some of the ants, perhaps the young ones, did not recognize them. Still they were never killed, or driven out of the nest, so that evidently when a mistake was made, it was soon recognized. No one who saw the different manner in which these ants and strangers were treated, could have the slightest doubt that the former were recognized as friends and the latter as enemies. The last three were put back on 14th May, 1877, that is to say, after a separation of a year and nine months, and yet they were amicably received, and evidently recognized as friends !

These observations were all made on *Formica fusca*, and it is of course possible that other species would behave in a different manner.

Indeed, in this respect *Lasius flavus* offers a surprising contrast to *F. fusca*. I was anxious to see whether the colonies of this species, which are very numerous round my house, were in friendly relations with one another With this view, I kept a nest of *L. flavus* for a day or two without food, and then gave them some honey, to which they soon found their way in numbers. I then put in the midst of them an ant of the same species from a neighbouring nest ; the others did not attack, but, on the contrary, cleaned her—though, from the attention she excited and the numerous communications which took place between her and them, I am satisfied that they knew she was not one of themselves. After a few minutes she accompanied some of the returning ants to the nest. They did not drag nor apparently guide her ; but she went with the rest freely. This I repeated several times with the same result.

I then took four ants, two from a nest about 500 yards from the first in one direction, the other from an equal distance in another. In all cases the result was the same. I then got a few from a colony about half a mile off. These also were most amicably received, and in every case the stranger went of her own accord to the nest. One of the strangers was, indeed, dragged about half way to the entrance of the nest, but was then left free and might have run away if she had liked. She, however, after wandering about for half an minute, voluntarily entered the nest. In one or two cases the stranger ran as quickly and straight to the nest as if she had been there over and over again. This, I suppose, can only have been by scent; and certainly no hounds in full cry could have pursued their game more directly or with less hesitation. In other cases, however, they were much longer before they went in. To satisfy myself that these facts were not owing to the nest having been taken from that of colonies or allies, I subsequently experimented with some ants of the same species from a nest in Hertfordshire; and they also behaved in a similar manner. In one or two cases they seemed to be attacked, though so feebly that I could not feel sure about it; but in no case were the ants killed.

The following fact surprised me still more. I put an ant (13th August) at 9 a.m. on a spot where a number of *Lasius flavus* (belonging to one of my nests of domesticated ants) had been feeding some hours previously, though none were there, or, indeed, out at all, at the moment. The entrance to the nest was about eight inches off; but she walked straight to it and into the nest. A second wandered about for four or five minutes, and then went in; a third, on the contrary, took a wrong direction, and, at any rate for three-quarters of an hour, did not find the entrance.

At that time, however, I did not ascertain what became of the specimens thus introduced into a strange community. I thought it would be worth while to determine this, so I subsequently (1881) took six ants from one of my nests of *L. flavus*, marked them, and introduced them into another nest of the same species. As in the preceding cases they entered quite readily; but though they were not at first attacked, they were evidently recognized as strangers. The others examined them carefully, and at length they were all driven out of the nest. Their greater readiness to enter a strange nest may perhaps be accounted for by the fact that, as a subterranean species their instinct always is to conceal themselves underground, whereas, *F. fusca*, a hunting species, does not do so except to enter its own nest.

How do these ants and bees recognize their companions ? The difficulty of believing that in such populous communities every individual knows every other by sight, has led some entomologists to suppose that each nest had a sign or passward. This was, for instance, the opinion of Gélieu, who believed that in each hive the bees had some common sign or password. As evidence of this, he mentions * that one of his hives had been for some days robbed by the bees from another : "et je désespérais de conserver cet essaim, lorsqu'un jour, sur le soir, je le vis fort inquiet, fort agité, comme s'il eût perdu sa reine. Les abeilles couraient en tout sens sur le devant et le tablier de la ruche, se flairant, se tâtant mutuellement, comme si elles eussent voulu se dire quelque chose. C'était pour changer leur signe de reconnaissance, qu'elles changèrent en effet pendant la nuit. Toutes les pillardes qui revinrent le lendemain, furent arrêtées et tuées. Plusieurs échappèrent aux gardes vigilantes qui défendaient l'entrée ; elles avertirent sans doute les autres du danger qu'elles avaient couru, et que l'on ne pouvait plus piller impunément. Aucune de celles qui voulurent recommencer leurs déprédations ne pénétra dans la ruche, dont elles avaient fait leur proie, et qui prospéra merveilleusement."

Dujardin doubts the explanation given by Gélieu. He thinks that the nest which was robbed was at that time queenless, and that the sudden change in the behaviour of the bees was due to their having acquired a queen.

Burmeister, on the contrary, in his excellent *Manual of Entomology*, says that "the power of communicating to their comrades what they purpose is peculiar to insects. Much has been talked of the so-called signs of recognition in bees, which is said to consist in recognizing their comrades of the same hive by means of peculiar signs. This sign serves to prevent any strange bee from entering into the same hive without being immediately detected and killed. It, however, sometimes happens that several hives

* *Le Conservateur des Abeilles*, p. 143.

have the same signs, when their several members rob each other with impunity. In these cases the bees whose hive suffers most alter their signs, and then can immediately detect their enemy." *

Others, again, have supposed a ts recognize one another by smell.

Mr McCook states that ants more or less soaked in water are no longer recognized by their friends, but, on the contrary, are attacked. Describing the following observation, he says †: "I was accidentally set upon the track of an interesting discovery. An ant fell into a box containing water placed at the foot of a tree. She remained in the liquid several moments and crept out. Immediately she was seized in a hostile manner, first by one, then another, then by a third: the two antennæ and one leg were thus held. A fourth ant assaulted the middle thorax and petiole. The poor little bather was thus dragged helplessly to and fro for a long time, and was evidently ordained to death. Presently I took up the struggling heap. Two of the assailants kept their hold; one finally dropped, the other I could not tear loose, and so put the pair back upon the tree, leaving the doomed immersionist to her hard fate."

After recording one or two other similar observations, he adds ‡: "The conclusion, therefore, seems warranted that the peculiar odour or condition by which the ants recognize each other was temporarily destroyed by the bath, and the individuals thus 'tainted' were held to be intruders, alien and enemy. This conclusion is certainly unfavourable to the theory that anything like an intelligent social sentiment exists among the ants. The recognition of their fellows is reduced to a mere matter of physical sensation or 'smell'." This conclusion does not, I confess, seem to me to be conclusively established.

* Burmeister's *Entomology*, p. 502.
† *Mound-making Ants of the Alleghanies*, p. 280.
‡ *Mound-making Ants of the Alleghanies*, p. 281.

We can hardly suppose that each ant has a peculiar odour, and it seems almost equally difficult, considering the immense number of ants' nests, to suppose that each community has a separate and peculiar smell. Moreover, in a previous chapter I have recorded some experiments made with intoxicated ants. It will be remembered that my ants are allowed to range over a table surrounded by a moat of water. Now, as already mentioned, out of forty-one intoxicated friends, thirty-two were carried into the nest and nine were thrown into the water; while out of fifty-two intoxicated strangers two were taken into the nest and fifty were thrown into the water. I think it most probable that even these two were subsequently brought out and treated like the rest.

It is clear, therefore, that in these species, and I believe in most, if not all others, the ants of a community all recognize one another. The whole question is full of difficulty. It occurred to me, however, that experiments with pupæ might throw some light on the subject. Although all the communities are deadly enemies, still if larvæ or pupæ from one nest are transferred to another, they are tended with apparently as much care as if they really belonged to the nest. In ant-warfare, though sex is no protection, the young are spared, at least when they belong to the same species. Moreover, though the habits of ants are greatly changed if they are taken away from their nest and kept with only a few friends, still, under such circumstances, they will carefully tend any young who may be confided to them. Now if the recognition were individual—if the ants knew any one of their comrades, as we know our friends, not only from strangers, but from one another—then young ants taken from the nest as pupæ and restored after they had come to maturity would not be recognized as friends. On the other hand, if the recognition were effected by means of some signal or password, then the pupæ which were entrusted to ants from another nest would have the password, if any, of that nest; and not of their own. Hence in this case they would be amicably received in the nest from which their nurses had been taken, but not in their own.

In the first place, therefore, I put, on 2nd September, 1877, some pupæ from one of my nests of *Formica fusca* with a couple of ants from the same nest. On the 27th I put two of the ants, which in the meantime had emerged from these pupæ, back into their own nest at 8.30 a.m., marking them with paint as usual. At 9 they seemed quite at home; at 9.30, ditto; at 10, ditto; and they were nearly cleaned. After that I could not distinguish them.

On the 29th another ant came out of the pupa-state; and on 1st October, at 7.45, I put her back into the nest. She seemed quite at home, and the others soon began to clean her. We watched her from time to time, and she was not attacked; but, the colour being removed, we could not recognize her after 9.30.

On 14th July last year (1878) I put into a small glass some pupæ from another nest of *Formica fusca* with two friends.

On 11th August I put four of the young ants which had emerged from these pupæ into the nest. After the interval of an hour, I looked for them in vain. The door of the nest was closed with cotton-wool; so that they could not have come out; and if any were being attacked, I think we must have seen it. I believe, therefore, that in the meantime they had been cleaned. Still, as we did not actually watch them, I was not satisfied. I put in, therefore, two more at 5 p.m. At 5.30 they were all right; at 5.45, ditto, one being almost cleaned. A 6 one was all right; the other was no longer recognizable, having been quite cleaned. At 6.30 also one was quite at home; the other could not be distinguished. At 7 both had been completely cleaned.

The following day I marked another, and put her in at 6 a.m. At 6.15 she was all right among the others, and also at 6.30, 7, 7.30, 8, and 9.30, after which I could no longer distinguish her.

Again, on the following day, I put in another at 6.45 a.m. At 7 she was quite at home, and also at 7.15, 7.30, 8, and to 9.30, after which I did not watch her.

To test the mode in which the ants of this nest would behave to a stranger, I then, though feeling no doubt as to the result, introduced one. The difference was very striking. The stranger was a powerful ant; still she was evidently uncomfortable, started away from every ant she met, and ran nervously about, trying to get out of the nest. She was, however, soon attacked.

Again, on 1st October, some pupæ of *Lasius niger* were placed in a glass with five ants from the same nest.

On 8th December I took three of the ants which had emerged from these pupæ, and at midday put them back into their old nest, having marked them by nicking the claws. Of course, under these circumstances we could not watch the ants. I examined the nest, however, every half hour very carefully, and am satisfied that there was no fighting. The next morning there was no dead ant; nor was there a death in the nest for more than a fortnight.

21st December.—Marked three more in the same manner, and put them in at 11.15 a.m. Looked at the usual intervals, but saw no fighting. The next morning there was no dead one outside the nest; but I subsequently found one of these ants outside, and nearly dead. I am, however, disposed to think that I had accidentally injured this ant.

23rd December.—Painted three, and put them in at 10 a.m. At 11 they were unmolested, 12 ditto, 1 ditto, 2 ditto, 3 ditto, 4 ditto, 5 ditto. At 3 I put in three strangers for comparison: two of them were soon attacked; the other hid herself in a corner; but all three were eventually dragged out of the nest. I found no other dead ant outside the nest for some days.

29th December.—Painted three more, and put them in at 10.30 a.m. At 11 they were unmolested, 12 ditto, 1 ditto, 2 ditto. During the afternoon they were once or twice attacked for a minute or two, but the ants seemed soon to perceive the mistake, and let them go again. The next morning I found one dead ant, but had no reason to suppose that she was one of the above three. The following morning there was again only one dead ant outside the nest; she was the third of the strangers put in on the 23rd, as mentioned above. Up to 23rd January found no other dead one.

3rd January, 1879.—Painted three more, and put them in at 11.30 a.m. At 12 two were all right: we could not see the third; but no ant was being attacked. 12 ditto. 1, all three are unmolested; 2 ditto; 5 ditto. As already mentioned, for some days there was no dead ant brought out of the nest.

5th January.—Painted three more and put them in at 11.30 a.m. At 12 two were all right among the others; I could not find the third; but no ant was being attacked. 12.30 ditto, 1 ditto, 2 ditto, 4 ditto. On the following morning I found two of them all right among the others. There was no dead ant.

13th January.—Painted three more and put them in at 12.30. At 1 they were all right. 2 ditto. 4, two were unmolested; I could not see the third, but she was not being attacked. The next morning, when I looked at the nest, one was just being carried, not dragged, out. The ant carried her about 6 inches and then put her down, apparently quite unhurt. She soon returned into the nest, and seemed to be quite amicably received by the rest. Another one of the three also seemed quite at home. The third I could not see; but up to 23rd January no dead one was brought out of the nest.

19th January.—Marked the last three of these ants, and put them into the nest at 9.30 a.m. They were watched continuously up to 1. At that time two of them had been almost completely cleaned. One was attacked for about a minute soon after 11, and another a little later; but with these exceptions they were quite amicably received, and seemed entirely at home among the other ants.

Thus every one of these thirty-two ants was amicably received.

These experiments, then, seem to prove that ants removed from a nest in the condition of pupæ, but tended by friends, if reintroduced into the parent nest, are recognized and treated as friends. Nevertheless the recognition does not seem to have been complete. In several cases the ants were certainly attacked, though only by one or two ants, not savagely, and only for a short time. It seemed as if, though recognized as friends by the great majority, some few, more ignorant or more suspicious than the rest, had doubts on the subject, which, however, in some manner still mysterious, were ere long removed. The case in which one of these marked ants was carried out of the nest may perhaps be explained by her having been supposed to be ill, in which case, if the malady is considered to be fatal, ants are generally brought out of the nest.

It now remained to test the result when the pupæ were confided to the care of ants belonging to a different nest, though, of course, the same species.

I therefore took a number of pupæ out of some of my nests of *Formica fusca* and put them in small glasses, with ants from another nest of the same species. Now, as already mentioned, if the recognition were effected by means of some signal or password, then, as we can hardly suppose that the larvæ or pupæ would be sufficiently intelligent to appreciate, still less to remember it, the pupæ which were intrusted to ants from another nest would have the password, if any, of that nest, and not of the one from which they had been taken. Hence, if the recognition were effected by some password or sign with the antennæ, they would be amicably received in the nest from which their nurses had been taken, but not in their own.

I will indicate the nests by the numbers in my note-book.

On 26th August last year I put some pupæ of *Formica fusca* from one of my nests (No. 36) with two workers from another nest of the same species. Two emerged from the chrysalis state on the 30th; and on 2nd September I put them, marked as usual, into their old nest (No. 36) at 9.30 a.m. At 9.45 they seemed quite at home, and had already been nearly cleaned. At 10.15 the same was the case, and they were scarcely distinguishable. After that I could no longer make them out; but we watched the nest closely, and I think I can undertake to say that if they had been attacked we must have seen it.

Another one of the same batch emerged on 18th August, but was rather crippled in doing so. On the 21st I put her into the nest (No. 36). This ant was at once attacked, dragged out of the nest, and dropped into the surrounding moat of water.

Again, on 14th July last year (1878) I put some pupæ of *Formica fusca* from nest No. 36 into a glass with three ants of the same species from nest No. 60.

On the 22nd I put an ant from one of these pupæ into her old nest (No. 36) at 9.30 a.m. She was attacked. At 10 she was being dragged about. 10.30 ditto. I regretted she was not watched longer.

8th August.—Put another ant which had emerged from one of these pupæ into her old nest (No. 36) at 7.45 a.m. At 8 she seemed quite at home among the others. 8.15 ditto, 8.30 ditto, 9 ditto, 9.30 ditto.

9th August.—Put two other young ants of this batch into their old nest (No. 36) at 7 a.m. At 7.15 they were all right. At 7.30 one of them was being dragged by a leg, but only, I think, to bring her under shelter, and was then let go. Young ants of this species, when the nest is disturbed, are sometimes dragged to a place of safety in this way. At 8.30 they were all right and nearly cleaned. After this I could not distinguish them ; but if they had been attacked, we must have seen it.

11th August.—Put in another one as before at 8.30 a.m. At 8.45 she was unmolested. At 9 she was dragged by a leg, like the last, but not for long ; and at 9.30 she was quite comfortable amongst the others. 10 ditto, 10.45 ditto, 12 ditto, 5 ditto.

24th August.—Put in the last two ants of this lot as before at 9.15 a.m. At 9.30 they were unmolested, 9.45 ditto. At 10 they were almost cleaned. At 10.30 I could only distinguish one ; and she had only a speck of colour left. She appeared quite at home ; and though I could no longer distinguish the other, I must have seen it if she had been attacked.

Thus, then, out of seven ants of this batch put back into their old nest, six were amicably received. On the other hand, I put one into nest No. 60, from which the three nurses were taken. She was introduced into the nest at 8.15 a.m., and was at once attacked. 8.45, she was being dragged about. 9 ditto, 9.15 ditto, 9.30 ditto. Evidently therefore she was not treated as a friend.

Again, on 14th July, 1878, I put some pupæ of *Formica fusca* from nest No. 60 with three ants from nest No. 36.

On 5th August at 4 p.m. I put an ant which had emerged from one of these pupæ into her old nest (No. 60). At 4.15 she seemed quite at home. They were already cleaning her ; and by 4.30 she was no longer distinguishable. We watched the nest, however, carefully for some time ; and I feel sure she was not attacked.

6th August.—Put another of this batch into nest No. 60 at 7.15 a.m. At 7.30 she was not attacked. At 8 one of the ants was carefully cleaning her. At 8.15 she was quite at home among the others. At 8.30 ditto ; she was nearly cleaned. 9.30 ditto.

8th August.—Put in another as before at 7.45. At 8 she was all right. 8.30 ditto, 9.30 ditto, 9.45 ditto.

9th August.—Put in another as before at 7 a.m. At

7.30 she is quite at home among the others, and already nearly cleaned. At 8 I could no longer distinguish her; but certainly no ant was being attacked. 9 ditto.

11th August.—Put in another as before at 8 a.m. At 8.15 she was quite at home. 8.30 ditto, 9 ditto, 9.30 ditto, 10 ditto, 12.30 ditto.

13th August.—Lastly, I put in the remaining young ant as before at 7 a.m. At 7.15 she was unmolested. At 7.30 ditto and nearly cleaned. At 8 I could no longer distinguish her; but no ant was being attacked.

Thus, then, as in the preceding experiment, these six ants when reintroduced into the nest from which they had been taken as pupæ, were received as friends. On the other hand, on 5th August I put a young ant of the same batch into nest No. 36, from which the three nurses had been taken. She was introduced at 11 and was at once attacked. At 11.30 she was being dragged about, and shortly after was dragged out of the nest. I then introduced a second; but she was at once attacked like the first.

22nd August.—I put some pupæ of *Formica fusca* from nest No. 64 under the charge of three ants from nest No. 60. By 7th September several young ones had emerged. I put two of them into nest No. 64 at 8.15 a.m. They were amicably received, as in the preceding experiments, and the ants began to clean them. At 8.30 they were all right. 8.45 ditto. At 9 they had been completely cleaned, so that I could not distinguish them; but there was no fighting going on in the nest.

On the same day, at 9.45 a.m., I put into nest 64 two more as before. At 10 they were both quite at home among the other ants. 10.15 ditto, 10.30 ditto, 11 ditto, 12 ditto, 1 ditto. I then put in a stranger; and she was at once fiercely attacked.

8th September.—Put in two more of the ants which had emerged from the pupæ, as before, at 9.30 a.m. At 9.45 they were all right. 10 ditto, 10.30 ditto, 11 ditto, 11.30 ditto, 12 ditto, 1 ditto.

On the other hand, on 14th September, I put one of these ants in the same manner into nest No. 60 at 6.30 a.m. She was at once attacked. At 6.45 she was being dragged about by an antenna. 7 ditto. At 7.30 she was by herself in one corner. At 8.30 she was again being dragged about. 9.30 ditto. The difference, therefore, was unmistakable.

Once more, on 29th July, I put some pupæ of *Formica fusca* from out of doors under the charge of three ants from nest No. 36.

3rd August.—Several had come out, and I put two of them into the nest of their nurses (No. 36) at 2 p.m. Both were at once attacked. At 2.45 they were being dragged about. 3 ditto. 3.30 one was being dragged about. 4, both were being attacked. Eventually one was turned out of the nest. The other I lost sight of.

4th August.—Put two more of this batch into nest No. 36, at 12.30. One was at once attacked. 1, one was being dragged about by an antennæ. 2.30, both were being attacked. At 2.45 one was dragged out of the nest.

I then put back one of the old ones; as might have been expected, she was received quite amicably.

I then tried the same experiment with another species, *Lasius niger*. I took some pupæ from two of my nests, which I knew not to be on friendly terms, and which I will call 1 and 2, and confided each batch to three or four ants taken from the other nest. When they had come to maturity I introduced them into the nests as before.

They were taken from their nest on 14th September; and the results were as follows.

Pupæ from nest 1 confided to ants from nest 2.

20th September.—Put one of the young ones into nest 2 at 7.15 a.m. Several at once threatened her. At 7.25 one of the ants seized her by an antenna, and began dragging her about. 7.30, she was still being dragged about. 8, ditto, 8.15, she was now being dragged about by three ants. 8.30, she was still attacked. 9, ditto. At 9.15 she was dragged out of the nest.

23rd September.—Put two of the young ants into nest 1 at 9.15 a.m. One was at once attacked, and the other a few minutes afterwards. 9.45, both were attacked. 10, ditto. One was now dead and hanging on to a leg of assailant. 10.15 ditto. 10.45, both were still being dragged about.

At 11 a.m. I put into nest 2 three more very young ones. At 11.10 one was attacked. At 11.20 all three were being viciously attacked, and yet one was nearly cleaned. At 12 one was being attacked, one was alone in a corner, the other we could not find. At 12.10 one was dragged out of the nest and then abandoned, on which, to my surprise, she ran into the nest again, which no old ant would have done. She was at once again seized by an antenna. At 12.30 she was still being dragged about; the second was being cleaned. In this instance, therefore, I think two out of the three were eventually accepted as inmates of the nest.

25th September.—Put two of the young ones into nest 1 at 2.30 p.m. At 2.45 one was attacked, but not viciously. 3 ditto, 3.15 ditto. No notice was taken of the other, though several ants came up and examined her. 3.30, the first was not attacked, the second was almost cleaned. 4, the first has been again attacked, but not viciously, and moreover has been partly cleaned. The second was evidently received as a friend, and was almost cleaned. 4.30, they are both comfortably among the others and are almost clean. At 5 I could no longer distinguish them.

I now pass to the other batch, namely, pupæ from nest 2 with ants from nest 1.

25th September.—Put three of the young ants into nest 1 at 9.30 a.m. At 9.45 two were attacked, the third was by herself. 10 ditto. At 10.15 one made her escape from the nest. At 10.20 the third was attacked. At 10.30 one of them was dragged out of the nest, and then abandoned. At 10.50 the third also was dragged out of the nest.

I then put two of these ants and a third young one into nest 2. At 11.15 a.m. they seemed quite happy; but at 11.30 two were being dragged about; the third, who was very young, was, on the contrary, being carefully cleaned. At 12 this last one was undistinguishable; of the other two, one was being attacked, the second was taken no notice of, though several ants came up to her. At 12.5 the first was dragged out of the nest and then abandoned; the second was being carefully cleaned. This went on till 12.20, when the paint was entirely removed.

27th September.—I put in three more of these young ants into nest 1, at 7.45 a.m. At 8 o'clock they seemed quite at home among the other ants. A few minutes after, one was being held by a leg; the other two seemed quite at home. At 8.30 one was almost cleaned, the other I could not see. At 9 two of them were quite at home, but I could not see the third. At 9.30 they were both nearly cleaned; and after that we were no longer able to distinguish them.

Thinking the results might be different if the ants were allowed to become older before being returned into their nests, I made no further observations with these ants for two months. I then took two of the ants which had emerged from the pupæ separated on 20th September, and which had been brought up by ants from nest 2, and on 22nd November I put them back at 12 a.m. in their old nest (that is to say, in nest 1), having marked them, as usual, with paint. They showed no signs of fear, but ran about among the other ants with every appearance of being quite at home. At 12.15 ditto. At 12.30 one was being cleaned. At 12.45 both were being cleaned; and by 1 o'clock they could scarcely be distinguished from the other ants. There had not been the slightest symptoms of hostility. After this hour we could no longer identify them; but the nest was carefully watched throughout the afternoon, and I think I can undertake to say that they were not attacked. When we left off watching, the nest was enclosed in a box. The next morning I examined it carefully to see if there were any dead bodies. This was not the case; and I am satisfied, therefore, that neither of these two ants was killed. To test these ants, I then, on 24th November, at 8.30 a.m., put into the nest two ants from nest 2. At 8.40 one was attacked; the other had hid herself away in a corner. At 9.15 both of the ants were being dragged about. At 9.35 one was dragged out of the nest and then released, and the other a few minutes afterwards. After watching them for some time to see that they remained outside, I restored them to their own nest. The contrast, therefore, was very marked.

Again, on 25th November, I took two ants which had emerged from pupæ belonging to nest 2, removed on 20th September, and brought up by ants from nest 1, and put them back into their old nest at 2 p.m. They were watched continuously until 4 p.m., but were not attacked, nor even threatened. The following morning one of them was quite well, the other one we could not distinguish; she had probably been cleaned. If she had been killed, we must have found her dead body. I then at 10 a.m. put in two more. At 10.30 one of them was attacked for a moment, but only for a moment. With this exception neither of them was attacked until 2 o'clock, when one of them was again seized and dragged about for a minute or two, but then released again. We continued watching them till half past 4, when they seemed quite at home amongst the others. On the other hand a stranger, put in as a test at 12, was at once attacked. It was curious, however, that although she was undoubtedly attacked, yet at the very same time another ant began to clean her.

The next morning we found one ant, and only one, in the box outside the nest; and this turned out to be the stranger of yesterday. She had been almost cleaned;

but there were one or two small particles of paint still remaining, so that there could be no doubt of her identity.

The next day, 27th November, I put in three more of the ants derived from these pupæ at 10 a.m. At 10.30 they were all right, running about amongst the others. At 11 o'clock the same was the case; but whilst I was looking again shortly afterwards, one of them was seized by an antenna and dragged a little way, but released again in less than a minute. Shortly afterwards one of the others was also seized, but let go again almost immediately. At one o'clock they were all right, and also at two. They had, however, in the meantime been more than once threatened, and even momentarily seized, though they were never dragged about as strangers would have been. At three o'clock I found one of them dead; but I think I must have accidentally injured her, and I do not believe that she was killed by the other ants, though I cannot speak quite positively about it. The other two were quite at home, and had been partly cleaned. At six one of them was running about comfortably amongst the rest; the other I could not distinguish; but certainly no ant was being attacked.

28th November.—I put in the last two ants from the above-mentioned batch of pupæ at noon. Like the preceding, these ants were occasionally threatened, and even sometimes attacked for a moment or two; but the other ants soon seemed to find out their mistake, and on the whole they were certainly treated as friends, the attacks never lasting more than a few moments. One of them was watched at intervals of half an hour until 5 p.m.; the other we could not distinguish after 3 p.m., the paint having been licked off; but we should certainly have observed it had she been attacked.

On the whole, then, all the thirty-two ants belonging to *Formica fusca* and *Lasius niger*, removed from their nest as pupæ, attended by friends and restored to their own nest, were amicably received.

What is still more remarkable, of twenty-two ants belonging to *F. fusca*, removed as pupæ, attended by strangers, and returned to their own nest, twenty were amicably received. As regards one I am doubtful; the last was crippled in coming out of the pupa-case; and to this perhaps her unfriendly reception may have been due.

Of the same number of *Lasius niger* developed in the same manner from pupæ tended by strangers belonging to the same species, and then returned into their own nest, nineteen were amicably received, three were attacked, and about two I feel doubtful.

On the other hand, fifteen specimens belonging to the same two species, removed as pupæ, tended by strangers belonging to the same species, and then put into the strangers' nest, were all attacked.

The results may be tabulated as follows:—

	Pupæ brought up by friends and replaced in their own nest.	Pupæ brought up by strangers.	
		Put in own nest.	Put in strangers' nest.
Attacked . .	0	7*	15
Received amicably	33	37	0

The differences cannot be referred to any difference of temperament in different nests. The specimens of *F. fusca* experimented with in August and September last were taken principally from two nests, numbered respectively 36 and 60. Now, while nest 36, in most cases, amicably received ants bred from its own pupæ but tended by ants from 60, it showed itself fiercely hostile to ants from pupæ born in nest 60, even when these had been tended by ants from nest 36. Nest 60, again, behaved in a similar manner; amicably receiving as a general rule, its own young, even when tended by ants from 36; and refusing to receive ants born in nest 36, even when tended by specimens from nest 60.

* I do not feel sure about three of these.

These experiments seem to indicate that ants of the same nest do not recognize one another by any password. On the other hand, they seem to show that if ants are removed from a nest in the pupa-state, tended by strangers, and then restored, some at least of their relatives are puzzled, and for a time doubt their claim to consanguinity. I say some, because while strangers under the circumstances would have been immediately attacked, these ants were in every case amicably received by the majority of the colony, and it was sometimes several hours before they came across one who did not recognize them.

In all these experiments, however, the ants were taken from the nest as pupæ, and though I did not think the fact that they had passed their larval existence in the nest could affect the problem, still it might do so. I determined therefore to separate a nest before the young were born, or even the eggs laid, and then ascertain the result. Accordingly I took one of my nests of *F. fusca*, which I began watching on 13th September, 1878, and which contained two queens, and on 8th February, 1879, divided it into halves, which I will call A and B, so that there were approximately the same number of ants with a queen in each division. At this season, of course, the nest contained neither young nor even eggs. During April both queens began to lay eggs. On 20th July I took a number of pupæ from each division and placed each lot in a separate glass, with two ants from the same division. On 30th August I took four ants from the pupæ bred in B, and one from those in A (which were not quite so forward), and after marking them as usual with paint, put the B ants into nest A, and the A ant into nest B. They were received amicably and soon cleaned. Two, indeed, were once attacked for a few moments, but soon released. On the other hand, I put two strangers into nest A, but they were at once driven out. For facility of observation I placed each nest in a closed box. On the 31st I carefully examined the nests and also the boxes in which I placed them.

I could only distinguish one of the marked ants, but there were no dead ants either in the nests or boxes.

I carefully examined the box in the same way for several successive mornings, but there was no dead ant. If there had been I must have found the body, and I am sure, therefore, that these ants were not attacked.

Again, on 31st August I put two more of the ants which had emerged from the pupæ taken out of nest B, and nursed by ants from that nest, into nest A at 10 a.m. At 10.30 a.m. they were quite comfortable amongst the others. At 11 a.m. I looked again and they seemed quite at home, as also at 11.30 a.m., after which for some time I looked every hour, and they were never attacked. The next morning I found them peaceably among the other ants.

On 15th September I put three of the ants which had emerged from the pupæ taken out of nest A, and nursed by ants from that nest, and put them into nest B at 1.30 p.m. They seemed to make themselves quite at home. I looked again at 2.30 p.m., with the same result. At 3.30 p.m. I could only find two, the third having no doubt been cleaned, but no ant was being attacked. At 5.30 p.m. they were no longer distinguishable, but if any one was being attacked we must have seen it. The next morning they all seemed quite peaceful, and there was no dead ant in the box. I looked again on the 17th and 19th, but could not distinguish them. As, however, there was no dead ant, they certainly had not been killed. I then put in a stranger; she was soon attacked and driven out of the nest—showing that, as usual, they would not tolerate an ant whom they did not recognize as in some way belonging to the community.

Again, on 10th April, 1881, I divided a two-queened nest of *Formica fusca*, leaving a queen in each half. At that time no eggs had yet been laid, and of course there were no larvæ or pupæ. In due course both queens laid eggs, and young ants were brought up in each half of the nest. I will call the two halves as before A and B.

On 15th August, at 9 a.m., I put three of the young ants from A into B, and three from B into A. At 9.30 a.m. none were attacked, 10 a.m. ditto, 10.30 a.m. ditto. One was being cleaned; 12 a.m. ditto, 2 p.m. ditto. In fact, they seemed quite at home with the other ants. The next morning I was unable to recognize them, the paint having been entirely removed. The ants were all peaceably together in the nest, and there were no dead ones either in the nest or in the outer box. It is evident, therefore, that they had been treated as friends.

17th August.—I put in three more from B into A at noon. At 12.30 p.m. they were with the other ants; at 1 p.m. ditto, at 2 p.m. ditto, at 3 p.m. ditto, at 5 p.m. ditto. The following morning I was still able to recognize them, though most of the paint had been removed. They also were evidently treated as part of the community.

19th September.—Put in three more from A into B at 8.30 a.m. I looked at them at intervals of half an hour, but none of them were attacked. Next morning there was no ant outside the nest, nor had any been killed.

10th October.—Put in three more at 7 a.m., and looked at intervals of an hour. They were not attacked, and evidently felt themselves among friends. The next morning I was still able to recognize two. There was no dead ant either in the nest or the outer box.

Lastly, on 15th October, I put in four more at 7 a.m., and watched them all day at short intervals. They exhibited no sign of fear, and were never attacked. In fact, they made themselves quite at home, and were evidently, like the preceding, recognized as friends. For the sake of comparison at noon I again put in a stranger. Her behaviour was in marked contrast. The preceding ants seemed quite at home walked about peaceably among the other ants, and made no attempt to leave the nest. The stranger, on the contrary, ran uneasily about, started away from any ant she met, and made every effort to get out of the nest. After she had three times escaped from the nest, I put her back with her own friends.

Thus, then, when a nest of *Formica fusca* was divided early in spring, and when there were no young, the ants produced in each half were in twenty-eight cases all received as friends. In no case was there the slightest trace of enmity.

These observations seem to me conclusive as far as they go, and they are very surprising. In the previous experiments, though the results were similar, still the ants experimented with had been brought up in the nest, and were only removed after they had become pupæ. It might therefore be argued that the ants having nursed them as larva, recognized them when they came to maturity; and though this would certainly be in the highest degree improbable, it could not be said to be impossible. In the present case, however, the old ants had absolutely never seen the young ones until the moment when, some days after arriving at maturity, they were introduced into the nest; and yet in twenty-one cases they were undoubtedly recognized as belonging to the community.

It seems to me, therefore, to be established by these experiments that the recognition of ants is not personal or individual; that their harmony is not due to the fact that each ant is individually acquainted with every other member of the community.

At the same time, the fact that they recognize their friends even when intoxicated, and that they know the young born in their own nest even when they have been brought out of the chrysalis by strangers, seems to indicate that the recognition is not effected by means of any sign or password.[40]

CHAPTER VII

POWER OF COMMUNICATION

The Social Hymenoptera, according to Messrs. Kirby and Spence,* "have the means of communicating to each other information of various occurrences, and use a kind of language which is mutually understood, . . . and is not confined merely to giving intelligence of the approach or absence of danger; it is also co-extensive with all their other occasions for communicating their ideas to each other."

Huber assures us as regards Ants † that he has "frequently seen the antennæ used on the field of battle to intimate approaching danger, and to ascertain their own party when mingled with the enemy; they are also employed in the interior of the ant-hill to apprise their companions of the presence of the sun, so favourable to the development of the larvæ, in their excursions and emigrating to indicate their route, in their recruitings to determine the time of departure", etc. Elsewhere also he says ‡ "that should an Ant fall in with any of her associates from the nest they put her in the right way by the contact of their antennæ."

These statements are most interesting; and it is much to be regretted that he has not given us in detail the evidence on which they rest. In another passage, indeed, he himself says,§ "If they have a language, I cannot give too many proofs of it." Unfortunately, however, the chapter which he devotes to this important subject is very short, and occupied with general statements rather than with the accounts of the particular

* *Introduction to Entomology*, ii, p. 50.
† Loc. cit., p. 206.
‡ Loc. cit., p. 157.
§ Loc. cit., p. 205.

experiments and observations on which those statements rest. Nor is there any serious attempt to ascertain the nature, character, and capabilities of this antennal language. Even if by motions of these organs Ants and Bees can caress, can express love, fear, anger, etc., it does not follow that they can narrate facts or describe localities.

The facts recorded by Kirby and Spence are not more explicit. It is therefore disappointing to read in the chapter especially devoted to this subject, that, as regards the power possessed by Ants and Bees to communicate and receive information, "it is only necessary to refer you to the endless facts in proof, furnished by almost every page of my letters on the history of Ants and of the Hive Bee. I shall therefore but detain you for a moment with an additional anecdote or two, especially with one respecting the former tribe, which is valuable from the celebrity of the narrator."

The first of these anecdotes refers to a Beetle (*Ateuchus pilularius*) which, having made for the reception of its eggs a pellet of dung too heavy for it to move, "repaired to an adjoining heap and soon returned with three of his companions. All four now applied their united strength to the pellet, and at length succeeded in pushing it out, which being done, the three assistant Beetles left the spot and returned to their own quarters." This observation rests on the authority of an anonymous German artist; and though we are assured that he was a "man of strict veracity", I am by no means satisfied that his explanation of what took place is correct. M. Fabre, in his interesting *Souvenirs Entomologiques*, records a similar observation, but explains it in another manner, and thus places the facts in a very different light.

The second case is related by Kalm, on the authority of Dr Franklin, but again does not seem to me to justify the conclusions drawn from it by Messrs. Kirby and Spence. Dr Franklin having found a number of ants in a jar of treacle, shook them out and suspended the jar "by a string from the ceiling. By chance one ant remained, which, after eating its fill, with some difficulty found its way up the string, and, thence reaching the ceiling, escaped by the wall to its nest. In less than half an hour a great company of ants sallied out of their hole, climbing the ceiling, crept along the string into the pot and began to eat again; this they continued until the treacle was all consumed, one swarm running up the string while another passed down. It seems indisputable that the one ant had in this instance conveyed news of the booty to his comrades, who would not otherwise have at once directed their steps in a body to the only accessible route." *

Elsewhere, Messrs. Kirby and Spence say †: "If you scatter the ruins of an ants' nest in your appartment, you will be furnished with another proof of their language. The ants will take a thousand different paths, each going by itself, to increase the chance of discovery; they will meet and cross each other in all directions, and perhaps will wander long before they can find a spot convenient for their reunion. No sooner does any one discover a little chink in the floor through which it can pass below than it returns to its companions, and, by means of certain motions of its antennæ, makes some of them comprehend what route they are to pursue to find it, sometimes even accompanying them to the spot; these, in their turn, become the guides of others, till all know which way to direct their steps."

Here, however, Messrs. Kirby and Spence do not sufficiently distinguish between the cases in which the ants were guided, from those in which they were directed to the place of safety. It is obvious, however, that the power of communication implied in the latter case is much greater than in the former.

A short but very interesting paper by Dujardin on this subject is contained in the *Annales des Sciences* for 1852. He satisfied himself that some bees which came to honey put out by him for the purpose "avaient

* Loc. cit., p. 422. † *Introd. to Entomology*, vol. ii, p. 6.

dû recevoir dans la ruche un avertissement porté par quelques-unes de celles qui étaient venues isolément, soit à dessein, soit par hasard." That no doubt might remain, he tried the following experiment, which he says, " me paraît tout-à-fait concluante. Dans l'épaisseur d'un mur latéral à 18 mètres de distance des ruches A et B, se trouve une niche pratiquée, suivant l'usage du pays, pour constater la mitoyenneté, et recouverte par un treillage et par une treille, et cachée par diverses plantes grimpantes. J'y introduisis, le 16 novembre, une soucoupe avec du sucre légèrement humecté ; puis j'allai présenter une petite baguette enduite de sirop à une abeille sortant de la ruche. Cette abeille s'étant cramponnée à la baguette pour sucer le sirop, je la transportai dans la niche sur le sucre, où elle resta cinq ou six minutes jusqu'à ce qu'elle se fut bien gorgée ; elle commença alors à voler dans la niche, puis deçâ et delà devant le treillage, la tête toujours tournée vers la niche, et enfin elle prit son vol vers la ruche, où elle rentra.

" Un quart d'heure se passa sans qu'il revînt une seule abeille à la niche ; mais, à partir de cet instant, elles vinrent successivement au nombre de trente, explorant la localité, cherchant l'entrée de la niche qui avait dû leur être indiquée, et où l'odorat ne pouvait nullement les guider, et, à leur tour vérifiant avant de retourner à la ruche, les signes qui leur feraient retrouver cette précieuse localité ou qui leur permettraient de l'indiquer à d'autres. Tous les jours suivants les abeilles de la ruche A vinrent plus nombreuses à la niche où j'avais soin de renouveler le sucre humecté, et pas une seule de la ruche B n'eut le moindre soupçon de l'existence de ce trésor et ne vint voler de ce côté. Il était facile, en effet, de constater que les premières se dirigeaient exclusivement de la ruche à la niche, et réciproquement." *

It is of course clear from these observations that the ants and bees accompanied their fortunate friends

* [For a modern explanation of these phenomena in bees, see the notes to Chapter X.—Ed.]

to the stores of food which they had discovered, but this really does not in itself imply the possession of any great intelligence.

That ants and bees have a certain power of communication cannot, indeed, be doubted. Several striking cases are mentioned by M. Forel. For instance, on one occasion an army of Amazon ants (*Polyergus rufescens*) was making an expedition to attack a nest of *F. rufibarbis.* They were not, however, quite acquainted with the locality. At length it was discovered: "Aussitôt," he observes, "un nouveau signal fût donné, et toutes les amazones s'élancèrent dans cette direction." On another occasion he says: "Je mis un gros tas de *T. cæspitum* d'une variété de grande taille à un décimètre d'un des nids d'une colonie de *Pheidole pallidula.* En un clin d'œil l'alarme fut répandue, et des centaines de Pheidole se jetèrent au-devant de l'ennemi."

The species of *Camponotus,* when alarmed, "non seulement se frappent vivement et à coups répétés les uns les autres, mais en même temps ils frappent le sol deux ou trois fois de suite avec leur abdomen, et répètent cet acte à de courts intervalles, ce qui produit un bruit très marqué qu'on entend surtout bien lorsque le nid est dans un tronc d'arbre." *

It would even seem, according to M. Forel, that some species understand the signs of others. Thus *F. sanguinea,* he says,† is able to seize "l'instant où les *pratensis* se communiquent le signal de la déroute, et elles savent s'apprendre cette découverte les unes aux autres avec une rapidité incroyable. Au moment même où l'on voit les *pratensis* se jeter les unes contre les autres en se frappant de quelques coups rapides, puis cesser toute résistance et s'enfuir en masse, on voit aussi les *sanguinea* se jeter tout-à-coup au milieu d'elles, sans la plus petite retenue, mordant à droite et à gauche comme des *Polyergus,* et arrachant des cocons de toutes les *pratensis* qui en portent."

* Loc. cit., p. 355. † Loc. cit., p. 359.

M. Forel is of opinion (p. 364) that the different species differ much in their power of communicating with one another. Thus, though *Polyergus rufescens* is rather smaller than *F. sanguinea*, it is generally victorious, because the ants of this species understand one another more quickly than those of *F. sanguinea*.

These statements are extremely interesting, and certainly appear to imply considerable intelligence. If, however, his inferences are correct, and the social Hymenoptera are really so highly gifted, it ought not to be necessary for us to rely on accidental observations; we ought to be able to test them by appropriate experiments.

Those which I have made with reference to bees will be described in a subsequent chapter.

Everyone knows that if an ant or a bee in the course of her rambles has found a supply of food, a number of others will soon make their way to the store. This, however, does not necessarily imply any power of describing localities. A very simple sign would suffice, and very little intelligence is implied, if the other ants merely accompany their friend to the treasure which she has discovered. On the other hand, if the ant or bee can describe the locality, and send her friends to the food, the case is very different. This point, therefore, seemed to me very important; and I have made a number of observations bearing on it.

The following may be taken as a type of what happens under such circumstances. On 12th June, 1874, I put a *Lasius niger*, belonging to a nest which I had kept two or three days without food, to some honey. She fed as usual, and then was returning to the nest, when she met some friends, whom she proceeded to feed. When she had thus distributed her stores, she returned alone to the honey, none of the rest coming with her. When she had a second time laid in a stock of food, she again in the same way fed several ants on her way towards the nest; but this time five of those so fed returned with her to the honey. In due course these five would no doubt have brought others, and so the number at the honey would have increased.

Some species, however, act much more in association than others—*Lasius niger*, for instance, much more than *Formica fusca*.

In March, 1877, I was staying at Arcachon. It was a beautiful and very warm spring day, and numerous specimens of *Formica fusca* were coursing about on the flagstones in front of our hotel. At about 10.45 a.m. I put a raisin down before one of them. She immediately began licking it, and continued till 11.2 a.m., when she went off almost straight to her nest, the entrance to which was about twelve feet away. In a few minutes she came out again, and reached the fruit, after a few wanderings, at about 11.18 a.m. She fed till 11.30 a.m., when she returned once more to the nest.

At 11.45 another ant accidentally found the fruit. I imprisoned her.

At 11.50 the first returned, and fed till 11.56, when she went off to the nest. On the way she met and talked with three ants, none of whom, however, came to the fruit. At 12.7 she returned, again alone, to the fruit.

On the following day I repeated the same experiment. The first ant went backwards and forwards between the raisin and the nest for several hours, but only six others found their way to it.

Again, on 11th July, 1875, I put out some pupæ in a saucer, and at 5.55 p.m. they were found by a *F. fusca*, who as usual carried one off to the nest.

At 6 p.m. she returned and took another. Again

6.1	,,	,,
6.3	,,	,,
6.4	,,	,,
6.5	,,	,,
6.6	,,	,,
6.7	,,	,,
6.8	,,	,,

At 6. 9 p.m. she returned and took another. Again

6.10	,,	,,
6.11	,,	,,
6.12	,,	,,
6.14	,,	,,
6.15	,,	,,
6.16	,,	,,
6.17	,,	,,
6.19	,,	,,
6.20	,,	,,
6.21	,,	,,
6.23	,,	,,
6.25	,,	,,
6.27	,,	,,
6.29	,,	,,
6.30	,,	,,
6.31	,,	,,
6.33	,,	,,
6.35	,,	,,
6.36	,,	,,
6.37	,,	,,
6.38	,,	,,
6.40	,,	,,
6.41	,,	,,
6.45	,,	,,
6.47	,,	,,
6.49	,,	,,
6.50	,,	,,
6.51	,,	,,
6.52	,,	,,
6.53	,,	,,
6.55	,,	,,
6.56	,,	,,
6.57	,,	,,
7. 0	,,	,,
7. 1	,,	,,
7. 2	,,	,,
7. 6	,,	,,

After these 45 visits, she came no more till 8 p.m.; but when I returned at 10 p.m. I found all the pupæ gone. During the time she was watched, however, she brought no other ant to assist.

I also made similar experiments with *Myrmica ruginodis* and *Lasius niger*, imprisoning (as before) all ants that came except the marked ones, and with similar results.[41]

No doubt it more frequently happens that if an ant or a bee discovers a store of food, others soon find their way to it, and I have been anxious to ascertain in what manner this is effected. Some have regarded the fact as a proof of the power of communication; others, on the contrary, have denied that it indicated any such power. Ants, they said, being social animals, naturally accompany one another; moreover, seeing a companion coming home time after time with a larva, they would naturally conclude that they also would find larvæ in the same spot. It seemed to me that it would be very interesting to determine whether the ants in question were brought to the larvæ, or whether they came casually. I thought therefore that the following experiment might throw some light on the question, viz.: to place several small quantities of honey in similar situations, then to bring an ant to one of them, and subsequently to register the number of ants visiting each of the parcels of honey, of course imprisoning for the time every ant which found her way to the honey except the first. If, then, many more came to the honey which had been shown to the first ant than to the other parcels, this would be in favour of their possessing the power of communicating facts to one another, though it might be said they came by scent. Accordingly, on 13th July, 1874, at 3 p.m., I took a piece of cork about 8 inches long and 4 inches wide, and stuck into it seventeen pins, on three of which I put pieces of card with a little honey. Up to 5.15 no ant had been up any of these pins. I then put an ant (*Lasius niger*) to the honey on one of the bits of card. She seemed to enjoy it, and fed for about five minutes, after which she went away. At 5.30 she returned, but went up six pins which had no honey on them. I then put her on to the card. In the meantime twelve other ants went up wrong pins and two up to the honey; these I imprisoned for the afternoon. At 5.46 my first ant went away. From that time to 6 o'clock seven ants came, but the first did not return. One of the seven went up a wrong pin, but seemed surprised, came down, and immediately went up to the right one. The other six went straight up the right pin to the honey. Up to 7 o'clock twelve more ants went up pins—eight right, and four wrong. At 7 two more went wrong. Then my first ant returned, bringing three friends with her; and they all went straight to the honey. At 7.11 she went home: on her way to the nest she met and accosted two ants, both of which then came straight to the right pin and up it to the honey. Up to 7.20 seven more ants came and climbed up pins—six right, and one wrong. At 7.22 my first ant came back with five friends; at 7.30 she went away again, returning at 7.45 with no less than twenty companions. During this experiment I imprisoned every ant that found her way up to the honey. Thus, while there were seventeen pins, and consequently sixteen chances to one, yet between 5.45 and 7.45 twenty-seven ants came, not counting those which were brought by the original ant; and out of these twenty-seven, nineteen went straight up the right pin. [Again, on four subsequent days] I put out the same piece of cork with ten pins, each with a piece of card and one with honey.

[These experiments, which were described in detail in Appendix D of earlier editions, gave the following results :—]

[On] July	13, out of	27 ants,	19 went	right and	8 wrong
,,	15	,, 29	,, 17	,,	12 ,,
,,	16	,, 30	,, 16	,,	14 ,,
,,	18	,, 26	,, 23	,,	3 ,,
,,	19	,, 45	,, 29	,,	16 ,,

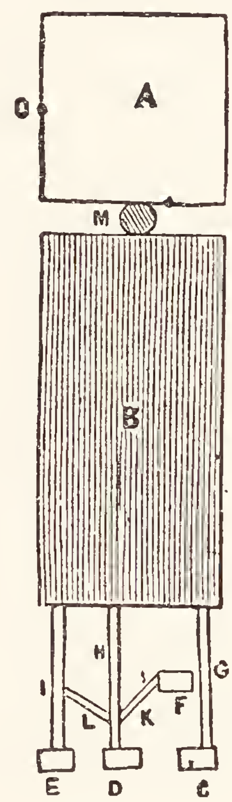
Or adding them all together, while there were never less than ten pins, out of 157 ants, 104 came up the right pin, and only 53 up the others.

I was at first disposed to infer from these facts that the first ant must have described the route to its friends, but subsequent observations satisfied me that they might have found their way by scent.

I then tried the following experiment :—

In Fig. 3, A is the ants' nest, O the door of the nest. M is the section of a pole on which the whole apparatus is supported. B is a board 2 feet long; C, D, E, and F are slips of glass connected with the board B by narrow strips of paper G, H, I. K is a movable strip of paper, $1\frac{1}{2}$ inch long, connecting the glass F with the strip H ; and L is another movable strip of paper, as nearly as possible similar, connecting H and I. On each of the slips of glass C and F I put several hundred larvæ of *L. flavus.* The object of the larvæ on C was to ascertain whether, under such circumstances, other ants would find the larvæ accidentally ; and I may say at once that none did so. I then put an ant (A), whom I had imprisoned overnight, to the larvæ on F. She took one, and knowing her way, went straight home over the bridge K and down the strip H. Now it is obvious that by always causing the marked ant (A) to cross the bridge K on a particular piece of paper, and if at other times the papers K and L were reversed, I should be able to ascertain whether other ants who came to the larvæ had had the direction and position explained to them ; or whether, having only been informed by (A) of the existence of the larvæ, they found their way to them by tracking (A)'s footsteps. If the former, they would in any case pass over the bridge K by whichever strip of paper it was constituted. On the other hand, if they found the larvæ by

Fig. 3.



tracking, then as the piece of paper by which (A) passed was transferred to L, it would mislead them and carry them away from the larvæ to I. In every case, then, I transposed the two papers forming the little bridges as soon as the ant (A) had crossed over K and L.

I put her (7th November, 1875) to the larvæ on F at 6.15 a.m. After examining them carefully, she returned to the nest at 6.34. No other ants were out; but she at once reappeared with four friends and reached the larvæ at 6.38. None of her friends, however, crossed the bridge; they went on to D, wandered about, and returned home. (A) returned to the larvæ at 6.47, this time with one friend, who also went on to D and returned without finding the larvæ.

7. 0	Ant (A) to larvæ.			
7. 8	,,	An ant at	7.10	went over L to I.
7.17	,,	with a friend, who at	7.21	,,
7.25	,,	with two friends, one of whom at	7.27	,,
7.32	,,	the other at	7.35	,,
7.39	,,	with a friend who went on to D, and then at	7.41	,,
7.46	Ant (A) to larvæ.	An ant at	7.42	went over L to I.
7.55	,,	,,	7.47	,,
8. 3	,,	,,	7.48	,,
8. 8	,,	,,	7.54	,,
8.19	,,	,,	7.57	,,
8.24	,,	,,	9.10	found the larvæ.
8.39	,,	,,	9.30	went over L to I.
8.50	,,			
9.12	,,			
9.22	,,			
9.40	,,			

9.47 Ant (A) to larvæ.
9.55 ,,
10.35 ,,

At 10.35 I imprisoned her till 12.30, when I put her again to the larvæ.

12.48	back to larvæ.			
12.55	,,	An ant at	12.58	went over L to I.
1.0	,,	,,	1. 1	,,
1.15	,,	,,	1.10	,,
1.20	,,	,,	1.13	,,

After this she did not come any more. During the time she made, therefore, 25 visits to the larvæ; 21 other ants came a distance of nearly 4 feet from the nest and up to the point of junction within 2 inches of the larvæ; but only one passed over the little bridge to the larvæ, while 15 went over the bridge L to I. On repeating this experiment with another marked ant, she herself made 40 journeys, during which 19 other ants found their way to the point of junction. Only 2 went over the little bridge to the larvæ, 8 went over L to I, and the remainder on to D.

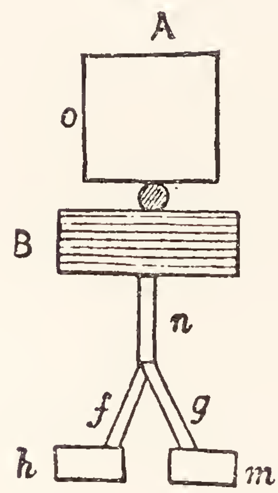
In another similar experiment the marked ant made 16 journeys; and during the same time 13 other ants came to the point of junction. Of these 13, 6 went on to D, 7 crossed over L to I, and not one found the larvæ. Altogether, out of 92 ants, 30 went on to D, 51 crossed over in the wrong direction to I, and only 11 found their way to the larvæ.

From 2nd January to 24th January (1875) I made a series of similar observations; and during this time 56 ants came in all. Of these, 20 went straight on to D, 26 across the paper to I, and only 10 to the larvæ.

This, I think, gives strong reason to conclude that, under such circumstances, ants track one another by scent.

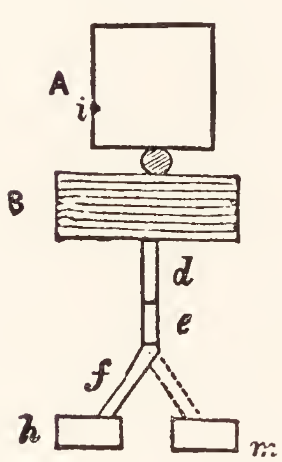
I then slightly altered the arrangements of the papers as shown in the accompanying diagram (Fig. 4). A, as before, is the nest, *o* being the door. B is the board; *h* is a glass on which are placed the larvæ; *m* is a similar glass, but empty; *n* a strip of paper: to the end of *n* are pinned two other strips *f* and *g*, in such a manner that they can be freely turned round, so that each can be turned at will either to *h* or *m*. Under ordinary circumstances the paper *f*, as in the figure, was turned to the larvæ; but whenever any ant, excepting the marked one, came, I turned the papers, so that *f* led to *m* and *g* to *h*. The result was striking. In all, 17 ants came, every one of whom took the wrong turn and went to *m*.

Fig. 4.



Although the observations above recorded seem to me almost conclusive, still I varied the experiments once more (see Fig. 5), making the connexion between the board B and the glass containing the larvæ by three separate but similar strips of paper, *d*, *e*, and *f*, as shown in the figure. Whenever, however, a strange ant came, I took up the strip *f* and rubbed my finger over it two or three times so as to remove any scent, and then replaced it. As soon as the stranger had reached the paper *e*, I took up the strip *d*, and placed it so as to connect *e* with the empty glass *m*. Thus I escaped the necessity of changing the paper *f*, and yet had a scented bridge between *e* and *m*. The details were given in the Appendix to the earlier editions, but have now been omitted to make way for other matter.

Fig. 5.



In this experiment the bridge over which the marked ant passed to the larvæ was left in its place, the scent, however, being removed or obscured by the friction of my finger; on the other hand, the bridge *d* had retained the scent, but was so placed as to lead away from the larvæ; and, under these circumstances, out of 41 ants which found their way towards the larvæ as far as *e*, 14 only passed over the bridge *f* to the larvæ, while 27 went over the bridge *d* to the empty glass *m*.

Taking these observations as a whole, 150 ants came to the point *e*, of which 21 only went on to the larvæ, while 95 went away to the empty glass. These experiments, therefore, seem to show that when an ant has discovered a store of food and others flock to it, they are guided in some cases by sight, while in others they track one another by scent.

I then varied the experiment as follows: I put an ant (*L. niger*) to some larvæ as usual, and when she knew her way, I allowed her to go home on her own legs; but as soon as she emerged from the nest, if she had any friends with her, I took her up on a bit of paper and carried her to the larvæ. Under these circumstances very few ants indeed found their way to them. Thus, on 23rd June, 1876, at 5.30, an ant which had been previously under observation was put to some larvæ. She took one and returned as usual to the nest. At 5.34 she came out with no less than 10 friends, and was then transferred to the larvæ. The others wandered about a little, but by degrees returned to the nest, not one of them finding their way to the larvæ. The first ant picked up a larva, returned, and again came out of the nest at 5.39 with 8 friends, when exactly the same thing happened. She again came out with companions at the undermentioned times:—

Hour.	Number of Friends.	Hour.	Number of Friends.
5.44	4	6. 1	5
5.47	4	6. 4	1
5.49	–	6. 7	–
5.52	–	6.11	3
5.54	5	6.14	4
5.57	2	6.17	6
5.59	2	6.20	–

Hour.	Number of Friends.	Hour.	Number of Friends.
6.23	5	7. 6	3
6.25	6	7. 8	3
6.29	8	7.10	5
6.32	2	7.13	–
6.35	–	7.17	3
6.42	4	7.19	7
6.44	–	7.21	5
6.46	3	7.24	–
6.49	2	7.26	3
6.56	–	7.29	1
6.59	–	7.31	2
7. 2	2	7.35	–
7. 4	–		

Thus during these two hours more than 120 ants came out of the nest in company with the one under observation. She knew her way perfectly; and it is clear that if she had been left alone, all, or at least most of, these ants would have accompanied her to the store of larvæ. Three of them were accidentally allowed to do so; but of the remainder, only 5 found their way to the larvæ; all the others, after wandering about a while, returned listlessly to the nest.

One of the ants which I employed in my experiments was under observation several days. I was, however, away from home most of the day, and when I left in the morning and went to bed at night I put her in a bottle; but the moment she was let out she began to work again. On one occasion I was away for a week, and on my return I let her out of the bottle, placing her on a little heap of larvæ about 3 feet from the nest. Under these circumstances I certainly did not expect her to return. However, though she had thus been six days in confinement, the brave little creature immediately picked up a larva, carried it off to the nest, and, after half an hour's rest, returned for another.

I conclude, then, that when large numbers of ants come to food they follow one another, being also to a certain extent guided by scent. The fact, therefore, does not imply any considerable power of intercommunication. There are, moreover, some other circumstances which seem to show that their powers in this respect are but limited. For instance, I have already mentioned that if a colony of *Polyergus* changes the situation of its nest, the mistresses are all carried to the new one by the slaves. Again, if a number of *F. fusca* are put in a box, and in one corner a dark place of retreat is provided for them with some earth, one soon finds her way to it. She then comes out again, and going up to one of the others, takes her by the jaws. The second ant then rolls herself into a heap, and is carried off to the place of shelter. They then both repeat the same manœuvre with other ants and so on until all their companions are collected together. Now it seems to me difficult to imagine that so slow a course would be adopted if they possessed any considerable power of descriptive communication.

On the other hand, there can, I think, be no doubt that they do possess some power of the kind.

This seems to me clearly shown by the following observations. In order, if possible, to determine whether the ants in question were brought to the larvæ, or whether they came casually, I tried (1875) the following experiments: I took three tapes, each about 2 ft. 6 in. long, and arranged them parallel to one another and about 6 inches apart. One end of each I attached to one of my nests (*L. niger*), and at the other end I placed a small glass. In the glass at the end of one tape I placed a considerable number (300 to 600) of larvæ. In the second I put two or three larvæ only; in the third none at all. The object of the last was to see whether many ants would come to the glasses under such circumstances by mere accident; and I may say at once that but few did so. I then took two ants and placed one of them to the glass with many larvæ, the other to that with two or three. Each of them took a larva and carried it to the nest, returning for another, and so on. After each journey I put another larva in the glass with only two or three larvæ, to replace that which had been removed. Now, if other ants came under the above circumstances as a mere matter of accident, or accompanying one another by chance, or if they simply saw the larvæ which were brought and consequently concluded that they might themselves also find larvæ in the same place, then the numbers going to the two glasses ought to be approximately equal. In each case the number of journeys made by the ants would be nearly the same; consequently, if it was a matter of scent, the two glasses would be in the same position. It would be impossible for an ant, seeing another in the act of bringing a larva, to judge for itself whether there were few or many larvæ left behind. On the other hand, if the friends were brought, then it would be curious to see whether more were brought to the glass with many larvæ, than to that which only contained two or three. I should also mention that, excepting, of course, the marked specimens, every ant which came to the larvæ was imprisoned until the end of the experiment.

The results of the above experiments are shown at a glance in the Table on page 133.

It must be admitted that this mode of observing is calculated to increase the number of friends brought by the ants to the glass with only 2 or 3 larvæ, for several reasons, but especially because in many cases an ant which had for some time had access to a glass with many larvæ was suddenly deprived of it, and it might well be that some time elapsed before the change was discovered. Some stray ants would, no doubt, in any case have found the larvæ; and we may probably allow for about 25 under this head. Again, some would, no doubt, casually accompany their friends; if we allow 25 also in this respect, we must deduct 50 from each side, and we shall have 254 against 54. Nevertheless, even without any allowances, the results seem to me

Tabular View of Experiments on Power of Communication.

Obser-vations.	Glass with many larvæ.			Glass with one or two larvæ.		
	Time occupied.	No. of journeys.	No. of friends.	Time occupied.	No of journeys.	No of friends.
	hours.			hours.		
1	1	7	11	—	—	—
2	—	—	—	1	6	0
3	—	—	—	2	13	8
4	—	—	—	3	24	5
5	3	38	22	1	10	3
6	2½	32	19	—	—	—
7	1	5	16	—	—	—
8	1½	11	21	3	23	2
9	—	—	—	1½	7	3
10	1	15	13	2	21	1
11	2	32	20	1	11	1
12	5	26	10	—	—	—
13	—	—	—	5	19	1
14	—	—	—	3	20	4
15	2½	41	3	2	5	0
16	1	10	16	2½	10	2
17	4½	53	2	4½	40	10
18	—	—	—	2	20	1
19	1	11	12	—	—	—
20	—	—	—	1	6	0
21	1½	20	15	4½	74	27
22	—	—	—	1½	25	4
23	4½	71	7	—	—	—
24	—	—	—	2	35	4
25	2	34	3	—	—	—
26	1½	35	21	2	18	0
27	2	37	9	1½	15	0
28	1½	9	10	2	14	0
29	2	37	5	1½	25	3
30	1½	9	10	2	14	0
31	2	37	5	1½	25	3
32	2	24	7	1	7	0
33	3½	43	17	3½	26	1
34	1	27	28	1	18	12
35	1	14	2	1	15	9
	52	678	304	59½	545	104

very definite. Some of the individual cases, especially perhaps experiments 9, 19, 20, 21 and 22, are very striking; and, taken as a whole, during 52 hours, the ants which had access to a glass containing numerous larvæ brought 304 friends; while during 59 hours those which were visiting a glass with only 2 or 3 larvæ brought only 104 to their assistance.

One case of apparent communication struck me very much. I had had an ant (*L. niger*) under observation one day, during which she was occupied in carrying off larvæ to her nest. At night I imprisoned her in a small bottle; in the morning I let her out at 6.15, when she immediately resumed her occupation. Having to go to London, I imprisoned her again at 9 o'clock. When I returned at 4.40, I put her again to the larvæ. She examined them carefully, but went home without taking one. At this time no other ants were out of the nest. In less than a minute she came out again with 8 friends, and the little troop made straight for the heap of larvæ. When they had gone two-thirds of the way, I again imprisoned the marked ant; the others hesitated a few moments, and then, with curious quickness, returned home. At 5.15 I put her again to the larvæ. She again went home *without a larvæ*, but, after only a few seconds' stay in the nest, came out with no less than 13 friends. They all went towards the larvæ; but when they got about two-thirds of the way, although the marked ant had on the previous day passed over the ground about 150 times, and though she had just gone straight from the larvæ to the nest, she seemed to have forgotten her way and wandered; and after she had wandered about for half an hour, I put her to the larvæ. Now in this case the 21 ants must have been brought out by my marked one, for they came exactly with her, and there were no other ants out. Moreover, it would seem that they must have been told, because (which is very curious in itself) she did not in either case bring a larva, and consequently it cannot have been the mere sight of a larva which induced them to follow her. I repeated an experiment similar to this more than once.

For instance, one rather cold day, when but few ants were out, I selected a specimen of *Aphænogaster testaceopilosa,* belonging to a nest which I had brought back with me from Algeria. She was out hunting about six feet from home, and I placed before her a large dead bluebottle fly, which she at once began to drag to the nest. I then pinned the fly to a piece of cork, in a small box, so that no ant could see the fly until she had climbed up the side of the box. The ant struggled, of course in vain, to move the fly. She pulled first in one direction and then in another, but, finding her efforts fruitless, she at length started off back to the nest empty-handed. At this time there were no ants coming out of the nest. Probably there were some few others out hunting, but for at least a quarter of an hour no ant had left the nest. My ant entered the nest, but did not remain there ; in less than a minute she emerged accompanied by 7 friends. I never saw so many come out of that nest together before. In her excitement the first ant soon distanced her companions, who took the matter with much more *sang-froid,* and had all the appearance of having come out reluctantly, or as if they had been asleep and were only half awake. The first ant ran on ahead, going straight to the fly. The others followed slowly and with many meanderings ; so slowly, indeed, that for twenty minutes the first ant was alone at the fly, trying in every way to move it. Finding this still impossible, she again returned to the nest, not chancing to meet any of her friends by the way. Again she emerged in less than a minute with 8 friends, and hurried on to the fly. They were even less energetic than the first party ; and when they found they had lost sight of their guide, they one and all returned to the nest. In the meantime several of the first detachment had found the fly, and one of them succeeded in detaching a leg, with which she returned in triumph to the nest, coming out again directly with 4 or 5 companions. These latter, with one exception, soon gave up the chase and returned to the nest. I do not think so much of this last case, because as the ant carried in a substantial piece of booty in the shape of the fly's leg, it is not surprising that her friends should some of them accompany her on her return; but surely the other two cases indicate a distinct power of communication.

Lest, however, it should be supposed that the result was accidental, I determined to try it again. Accordingly on the following day I put another large dead fly before an ant belonging to the same nest, pinning it to a piece of cork as before. After trying in vain for ten minutes to move the fly, my ant started off home. At that time I could only see two other ants of that species outside the nest. Yet in a few seconds, considerably less than a minute, she emerged with no less than 12 friends. As in the previous case, she ran on ahead, and they followed very slowly and by no means directly, taking, in fact, nearly half an hour to reach the fly. The first ant, after vainly labouring for about a quarter of an hour to move the fly, started off again to the nest. Meeting one of her friends on the way she conversed with her a little, then continued towards the nest, but, after going about a foot, changed her mind, and returned with her friend to the fly. After some minutes, during which two or three other ants came up, one of them detached a leg, which she carried off to the nest, coming out again almost immediately with six friends, one of whom, curiously enough, seemed to lead the way, tracing it, I presume, by scent. I then removed the pin, and they carried off the fly in triumph.

Again, on 15th June, 1878, another ant belonging to the same nest had found a dead spider, about the same distance from the nest. I pinned down the spider as before. The ant did all in her power to move it; but after trying for twelve minutes, she went off to the nest. Although for a quarter of an hour no other ant had left the nest, yet in a few seconds she came out again with

10 companions. As in the preceding case, they followed very leisurely. She ran on ahead and worked at the spider for ten minutes; when, as none of her friends had arrived to her assistance, though they were wandering about, evidently in search of something, she started back home again. In three-quarters of a minute after entering the nest she reappeared, this time with 15 friends, who came on somewhat more rapidly than the preceding batch, though still but slowly. By degrees, however, they all came up, and after most persevering efforts carried off the spider piecemeal. On 7th July, I tried the same experiment with a soldier of *Pheidole megacephala*. She pulled at the fly for no less than fifty minutes, after which she went to the nest and brought five friends exactly as the *Aphænogaster* had done.

In the same way, one afternoon at 6.20 I presented a slave of *Polyergus* with a dead fly pinned down. The result was quite different. My ant pulled at the fly for twenty-five minutes, when, as in the previous cases, she returned to the nest. There she remained four or five minutes, and then came out again alone, returned to the fly, and again tried to carry it off. After working fruitlessly for between twenty and twenty-five minutes, she again went back to the nest, staying there four or five minutes, and then returning by herself to the fly once more. I then went away for an hour, but on my return found her still tugging at the fly by herself. One hour later again I looked, with the same result. Shortly afterwards another ant wandering about found the fly, but obviously, as it seemed to me, by accident.

At 3 o'clock on a subsequent day I again put a dead fly pinned on to a bit of cork before a *Formica fusca*, who was out hunting. She tried in vain to carry it off, ran round and round, tugged in every direction, and at length at ten minutes to four she returned to the nest: very soon after she reappeared preceded by one and followed by two friends; these, however, failed to discover the fly, and after wandering about a little returned to the nest. She then set again to work alone, and in about forty minutes succeeded in cutting off the head of the fly, which she at once carried into the nest. In a little while she came out again, this time accompanied by five friends, all of whom found their way to the fly; one of these, having cut off the abdomen of the fly, took it into the nest, leaving three of her companions to bring in the remainder of their prey.

These experiments certainly seemed to indicate the possession by ants of something approaching to language.[42] It is impossible to doubt that the friends were brought out by the first ant; and as she returned empty-handed to the nest, the others cannot have been induced to follow her merely by observing her proceedings. In face of such facts as these, it is impossible not to ask ourselves how far are ants mere exquisite automatons; how far are they conscious beings?[43] When we see an ant-hill, tenanted by thousands of industrious inhabitants, excavating chambers, forming tunnels, making roads, guarding their home, gathering food, feeding the young, tending their domestic animals, each one fulfilling its duties industriously, and without confusion, it is difficult altogether to deny to them the gift of reason[44]; and the preceding observations tend to confirm the opinion that their mental powers differ from those of men, not so much in kind as in degree.

CHAPTER VIII

ON THE SENSES OF ANTS

The Sense of Vision

It is, I think, generally assumed not only that the world really exists as we see it, but that it appears to other animals pretty much as it does to us. A little consideration, however, is sufficient to show that this is very far from being certain, or even probable.

In the case of insects, moreover, the mode of vision is still an enigma. They have, at least many of them have, a large compound eye on each side; and ocelli, generally three in number, situated on the summit of the head. The compound eyes consist of a number of facets, each situated at the summit of a tube, to the base of which runs a fibre of the optic nerve.

The structure of the ocellus and that of the compound eye are essentially different, and it does not seem possible that either the ocellus should be derived from the compound eye, or the compound eye from the ocellus. On the contrary, both seem to point back to a less developed ancestral type. Starting from such an origin, an increase of the separate elements and an improvement of the lens would lead to the ocellus, while an increase of the number of eyes would bring us to the compound eye.

On the other hand, it must be admitted that there are reasons for considering the different kinds of eyes to be of perfectly distinct origin. The eye of *Limulus*, according to Grenacher, is formed on a plan quite unlike that of other Crustacea. Again, the development of the eye in *Musca*, to judge from Weismann's observations, is very dissimilar from that of other insects. The varied position of the eye in different groups, as, for instance, in *Pecten, Spondylus, Euphausia, Onchidium,* etc., point to the same conclusion.

It seems clear that the image produced by the ocelli must be altogether different from the picture given by the compound eyes ; and we may therefore reasonably conclude that the two organs have distinct functions. It used formerly to be supposed that the compound eyes were intended for distant, the ocelli for near vision. Claparède, however, has maintained the opposite theory, while Mr Lowne regards the ocelli as incapable of producing "anything worthy the name of an image", and suspects that their function "is the perception of the intensity in the direction of light, rather than vision".

The ocelli, or simple eyes, probably see in the same manner as ours do. That is to say, the lens throws an image on the back of the eye, which we call the retina. In that case they would see everything really reversed, as we do ; though long practice has given us the right impression. The simple eye of insects thus resembles ours in this respect.[45]

As regards the mode of vision of the compound eyes, there are two distinct theories. According to one—the mosaic theory of Müller—each facet takes in only a small portion of the field ; while according to the other, each facet acts as a separate eye.

This latter view has been maintained by many high authorities, but it is difficult to understand how so many images could be combined into one picture. Some insects have more than 20,000 facets on each side of their head. No ants, indeed, have so many, but in some—as, for instance, in the males of *Formica pratensis*—there are not less than 1,000. The theory, moreover, presents some great anatomical difficulties. Thus, in certain cases there is no lens, and consequently there can be no image ; in some it would seem that the image would be formed completely behind the eye, while in others again it would be in front of the receptive surface. Another difficulty is that any true projection of an image would in certain species be precluded by the presence of impenetrable pigment, which only leaves a minute central passage for the light-rays. Again, it is urged that even the sharpest image would be useless, from the absence of a suitably receptive surface ; since the structure of the receptive surface corresponding to each facet seems to preclude it from receiving more than a single impression.

The prevailing opinion of entomologists now is that each facet receives the impression of one pencil of rays ; so that, in fact, the image formed in a compound eye is a sort of mosaic.

On the other hand, this theory itself presents great difficulties. Those ants which have very few facets must have an extremely imperfect vision. Again, while the image produced on the retina of the ocellus must of course be reversed as in our own eyes ; in the compound eyes, on the contrary, the vision would, on this theory, be direct. That the same animal should see some things directly, and others reversed ; and yet obtain definite conceptions of the outer world, would certainly be very remarkable.

In fact, these, so far fortunate, insects realize the epigram of Plato—

> Thou lookest on the stars, my love,
> Ah, would that I could be
> Yon starry skies, with thousand eyes
> That I might look on thee !

But if the male of *F. pratensis* sees 1,000 queens at once, when only one is really present, this would seem to be a bewildering privilege, and the prevailing opinion among entomologists is, as already mentioned, that each facet only takes in a portion of the object.[46]

But while it is difficult to understand how ants see, it is clear that they do see.

From the observations of Sprengel there could of course be little, if any, doubt that bees are capable of distinguishing colours ; and I have proved experimentally, as will be shown in a subsequent chapter, that this is the case. Under these circumstances, I have been naturally anxious to ascertain, if possible, whether the same holds good with ants. I have, however, found more difficulty in doing so because, as shown in the observations just recorded, ants find their food so much more by smell than by sight.

This being so, I could not apply to ants those tests which had been used in the case of bees. At length, however, it occurred to me that I might utilize the dislike which ants, when in their nests, have to light. Of course, they have no such feeling when they are out in search of food; but if light is let in upon their nests, they at once hurry about in search of the darkest corners, and there they all congregate. If, for instance, I uncovered one of my nests and then placed an opaque substance over one portion, the ants invariably collected in the shaded part.

I procured, therefore, four similar strips of glass, coloured respectively green, yellow, red, and blue, or rather, violet. The yellow was rather paler in shade, and that glass consequently rather more transparent than the green, which, again, was rather more transparent than the red or violet. I also procured some coloured solutions.

Prof. Dewar was kind enough to test my glasses and solutions with reference to their power of transmitting colour. Taking the wave-length of the extreme visible red as 760 and that of the extreme violet as 397, we have

760	to	647	give	red.
647	,,	585	,,	orange.
585	,,	575	,,	yellow.
575	,,	497	,,	green.
497	,,	455	,,	blue.
445	,,	397	,,	violet.

The result of his examination of my glasses and solutions was as follows:—

The light-yellow glass cut off the high end down to wave-length 442.

The dark-yellow glass cut off the high end down to wave-length 493.

The green glass cut off the high end down to wave-length 465, and also the red to 616.

The red glass cut off the high end down to wave-length 582.

The violet glass cut off the orange and yellow from wave-length 684 to 583, and a band between wave-lengths 543 and 516.

The purple glass cut off the high end down to wave-length 528.

The solution of chromate of potash cut off the high end to 507.

The saffron cut off the high end to about 473.

The blue fluid cut off the low end to 516.

The red fluid cut off the high end to 596.

I then (15th July, 1876) laid the strips of glass on one of my nests of *Formica fusca*, containing about 170 ants. These ants, as I knew, by many previous observations, seek darkness, at least when in the nest, and would collect in the darkest part. I then, after counting the ants under each strip, moved the glasses, at intervals of about half an hour, so that each should by turns cover the same portion of the nest. The results were as follows—the numbers indicating the approximate numbers of ants under each glass (there were sometimes a few not under any of the strips of glass) :—

1.	Green.	Yellow.	Red.	Violet.
	50	40	80	0
2.	Violet.	Green.	Yellow.	Red.
	0	20	40	100
3.	Red.	Violet.	Green.	Yellow.
	60	0	50	50
4.	Yellow.	Red.	Violet.	Green.
	50	70	1	40
5.	Green.	Yellow.	Red.	Violet.
	30	30	100	0
6.	Violet.	Green.	Yellow.	Red.
	0	14	5	140

7.	Red.	Violet.	Green.	Yellow.
	50	0	40	70
8.	Yellow.	Red.	Violet.	Green.
	40	50	1	70
9.	Green.	Yellow.	Red.	Violet.
	60	35	65	0
10.	Violet.	Green.	Yellow.	Red.
	1	50	40	70
11.	Red.	Violet.	Green.	Yellow.
	50	2	50	60
12.	Yellow.	Red.	Violet.	Green.
	35	55	0	70

Adding these numbers together, there were, in the twelve observations, under the red 890, under the green 544, under the yellow 495, and under the violet only 5. The difference between the red and the green is very striking, and would doubtless have been more so, but for the fact that when the colours were transposed the ants which had collected under the red sometimes remained quiet, as, for instance, in cases 7 and 8. Again, the difference between the green and yellow would have been still more marked but for the fact that the yellow always occupied the position last held by the red, while, on the other hand, the green had some advantage in coming next the violet. In considering the difference between the yellow and green, we must remember also that the green was decidedly more opaque than the yellow.

The case of the violet glass is more marked and more interesting. To our eyes the violet was as opaque as the red, more so than the green, and much more so than the yellow. Yet, as the numbers show, the ants had scarcely any tendency to congregate under it. There were nearly as many under the same area of the uncovered portion of the nest as under that shaded by the violet glass.

Lasius flavus also showed a marked avoidance of the violet glass.

I then experimented in the same way with a nest of *Formica fusca*, in which there were some pupæ, which were generally collected in a single heap. I used glasses coloured dark yellow, dark green, light yellow, light green, red, violet, and dark purple. The colours were always in the preceding order, but, as before, their place over the nest was changed after every observation.

To our eyes the purple was almost black, the violet and dark green very dark and quite opaque; the pupæ could be dimly seen through the red, rather more clearly through the dark yellow and light green, while the light yellow were almost transparent. There were about 50 pupæ, and the light was the ordinary diffused daylight of summer.

These observations showed a marked preference for the greens and yellows. The pupæ were 6½ times under dark green, 3 under dark yellow, 3½ under red, and once each under light yellow and light green, the violet and purple being altogether neglected.

I now tried the same ants under the same colours, but in the sun; and placed a shallow dish containing some 10 per cent solution of alum sometimes over the yellow, sometimes over the red. I also put four thicknesses of violet glass, so that it looked almost black.

Under the circumstances, the pupæ were placed under the red 7 times, dark yellow 5, once they were half under each, but never under the violet, purple, light yellow, dark or light green.

The following day I placed over the same nest, in the sun, dark green glass, dark red, and dark yellow. In nine observations the pupæ were carried three times under the red and nine times under the yellow.

I then tried a similar series of experiments with *Lasius niger*, using a nest in which were about 40 pupæ, which were generally collected in a single heap all together. As before, the glasses were moved in regular order after each experiment; and I arranged them so that the violet followed the red. As far, therefore, as position was concerned, this gave violet rather the best place. The glasses used were dark violet, dark red, dark green, and yellow, the yellow being distinctly the most transparent to our eyes.

Experiment			Experiment		
1.	Pupæ under	yellow.	17.	Pupæ under	yellow.
2.	,,	,,	18.	,,	,,
3.	,,	,,	19.	,,	red.
4.	,,	,,	20.	,,	,,
5.	,,	,,	21.	,,	yellow.
6.	,,	,,	22.	,,	,,
7.	,,	green.	23.	,,	,,
8.	,,	,,	24.	,,	red.
9.	,,	red.	25.	,,	yellow.
10.	,,	yellow.	26.	,,	red.
11.	,,	red.	27.	,,	,,
12.	,,	yellow.	28.	,,	,,
13.	,,	,,	29.	,,	,,
14.	,,	red.	30.	,,	yellow.
15.	,,	,,	31.	,,	red.
16.	,,	,,	32.	,,	green.

I now put two extra thicknesses of glass over the red and green.

33.	Pupæ under	red.	37.	Pupæ under	red.
34.	,,	yellow.	38.	,,	,,
35.	,,	red.	39.	,,	yellow.
36.	,,	yellow.	40.	,,	red.

The result is very striking, and in accordance with the observations on *Formica fusca*. In 40 experiments the pupæ were carried under the yellow 19 times, under the red 16 times, and under the green 5 times only, while the violet was quite neglected. After the first twenty observations, however, I removed it.

I then tried a nest of *Cremastogaster scutellaris* with violet glass, purple glass, and red, yellow, and green solutions, formed respectively with fuchsine, bichromate of potash, and chloride of copper. The purple looked almost black, the violet very dark: the red and green, on the contrary, very transparent, and the yellow even more so. The yellow was not darker than a tincture of saffron. The latter indeed, to my eye, scarcely seemed to render the insects under them at all less apparent; while under the violet and purple I could not trace them at all. I altered the relative positions as before. The nest contained about 50 larvæ and pupæ.

I made thirteen trials, and in every case the larvæ and pupæ were brought under the yellow or the green—never once under any of the other colours.

Again, over a nest of *Formica fusca* containing about 20 pupæ I placed violet glass, purple glass, a weak solution of fuchsine (carmine), the same of chloride of copper (green), and of bichromate of potash (yellow, not darker than saffron).

I made eleven trials, and again, in every case the pupæ were brought under the yellow or the green.

I then tried a nest of *Lasius flavus* with the purple glass, violet glass, very weak bichromate of potash, and chloride of copper as before.

With this species, again, the results were the same as in the previous cases.

In all these experiments, therefore, the violet and purple light affected the ants much more strongly than the yellow and green.

It is curious that the coloured glasses appear to act on the ants (speaking roughly) as they would, or, I should rather say, inversely, as they would, on a photographic plate. It might even be alleged that the avoidance of the violet glass by the ants was due to their preferring rays transmitted by the other glasses. From the habits of these insects such an explanation would be very improbable. If, however, the preference for the other coloured glasses to the violet was due to the transmission and not to the absorption of rays—that is to say, if the ants went under the green rather than the violet because the green transmitted rays which were agreeable to the ants, and which the violet glass, on the contrary, stopped—then, if the violet was placed over the other colours, they would become as distasteful to the ants as the violet itself. On the contrary, however, whether the violet glass was placed over the others or not, the ants equally readily took shelter under them. Obviously, therefore, the ants avoid the violet glass because they dislike the rays which it transmits.

But though the ants so markedly avoided the violet glass, still, as might be expected, the violet glass certainly had some effect, because if it were put over the nest alone, the ants preferred being under it to being under the plain glass only.

I then compared the violet glass with a solution of ammonio-sulphate of copper, which is very similar in colour, though perhaps a little more violet, and arranged the depth of the fluid so as to make it as nearly as possible of the same depth of colour as the glass.

Approx. number of Ants under the	Exp. 1.	Exp. 2.	Exp. 3.	Exp. 4.	Exp. 5.	Exp. 6.	Exp. 7.	Exp. 8.	Exp. 9.	Exp. 10.	Total.
Glass .	0	0	0	2	0	2	0	2	3	0	9
Solution .	40	80	100	80	50	70	60	40	90	100	710

In another experiment with *Lasius niger* I used the dark yellow glass, dark violet glass, and a violet solution of 5 per cent ammonio-sulphate of copper, diluted so as to be, to my eye, of exactly the same tint as the violet glass; in 8 observations the pupæ were three times under the violet solution, and 5 times under the yellow glass. I then removed the yellow glass, and in 10 more observations the pupæ were always brought under the solution.

It is interesting that the glass and the solution should affect the ants so differently, because to my eye the two were almost identical in colour. The glass, however, was more transparent than the solution.

To see whether there would be the same difference between red glass and red solution as between violet glass and violet solution, I then (Aug. 21) put over a nest of *Formica fusca* a red glass and a solution of carmine, as nearly as I could make it of the same tint. In 10 experiments, however, the ants were, generally speaking, some under the solution and some under the glass, in, moreover, as nearly as possible equal numbers.

20th August.—Over a nest of *Formica fusca* containing 20 pupæ, I placed a saturated solution of bichromate of potash, a deep solution of carmine, which let through scarcely any but the red rays, and a white porcelain plate.

Obs.								
1.	Under the bichr. of potash were	0	pupæ,	carmine	18,	porcelain	2
2.	,, ,,	0	,,	,,	6	,,	14
3.	,, ,,	6	,,	,,	3	,,	11
4.	,, ,,	0	,,	,,	5	,,	18
5.	,, ,,	6	,,	,,	4	,,	10
6.	,, ,,	0	,,	,,	19	,,	1
7.	,, ,,	0	,,	,,	0	,,	20
8.	,, ,,	4	,,	,,	15	,,	1
9.	,, ,,	2	,,	,,	4	,,	14
10.	,, ,,	0	,,	,,	4	,,	16
11.	,, ,,	0	,,	,,	3	,,	17
	Total . . .	18			81		124

I then put over another nest of *Formica fusca* four layers of red glass (which, when examined with the spectroscope, let through red light only), four layers of green glass (which, examined in the same way, transmitted nothing but a very little green), and a porcelain plate. Under these circumstances the ants showed no marked preference, but appeared to feel equally protected, whether they were under the red glass, the green glass, or the porcelain.

Thus, though it appears from other experiments that ants are affected by red light, still the quantity that passes through dark red glass does not seem greatly to disturb them. I tested this again by placing over a nest containing a queen and about 10 pupæ a piece of opaque porcelain, one of violet and one of red glass, all of the same size. The result is shown below.

1.	Queen went under	red glass	5	pupæ were taken under red glass	2	under porcelain
2.	,,	porcelain	0	,,	7	,,
3.	,,	red glass	0	,,	7	,,
4.	,,	,,	6	,,	2	,,
5.	,,	,,	6	,,	2	,,
6.	,,	,,	3	,,	7	,,
7.	,,	,,	10	,,	0	,,
8.	,,	,,	4	,,	6	,,
9.	,,	,,	1	,,	0	,,
10.	,,	porcelain	0	,,	10	,,
11.	,,	red glass	10	,,	0	,,
12.	,,	porcelain	4	,,	6	,,
13.	,,	red glass	7	,,	3	,,
14.	,,	porcelain	4	,,	6	,,
15.	,,	red glass	4	,,	6	,,
16.	,,	porcelain	0	,,	10	,,
17.	,,	red glass	10	,,	0	,,
18.	,,	,,	8	,,	2	,,
19.	,,	porcelain	7	,,	3	,,
20.	,,	,,	1	,,	9	,,
	Total . .		90		88	

Obviously, therefore, the ants showed no marked preference for the porcelain. On one, but only on one occasion (Obs. 9), most of the pupæ were carried under the violet glass, but generally it was quite neglected.

I now tried a similar experiment with porcelain and yellow glass.

Obs.				
1.	Queen went under porcelain	8 pupæ were taken under yellow	2 under porcelain	
2.	,, ,,	2	,,	8 ,,
3.	,, ,,	8	,,	2 ,,
4.	,, yellow glass	5	,,	5 ,,
5.	,, porcelain	3	,,	8 ,,
6.	,, yellow glass	8	,,	3 ,,
7.	,, porcelain	6	,,	5 ,,
8.	,, ,,	0	,,	7 ,,
9.	,, ,,	0	,,	10 ,,
10.	,, yellow glass	5	,,	5 ,,
11.	,, porcelain	8	,,	2 ,,
12.	,, ,,	3	,,	7 ,,
13.	,, yellow glass	10	,,	0 ,,
14.	,, porcelain	0	,,	10 ,,
15.	,, yellow glass	10	,,	0 ,,
16.	,, ,,	7	,,	3 ,,
17.	,, ,,	10	,,	0 ,,
18.	,, porcelain	1	,,	9 ,,
19.	,, ,,	0	,,	10 ,,
		98		92

The porcelain and yellow glass seemed, therefore, to affect the ants almost equally.

I then put two ants on a paper bridge, the ends supported by pins, the bases of which were in water. The ants wandered backwards and forwards, endeavouring to escape. I then placed the bridge in the dark and threw the spectrum on it, so that successively the red, yellow, green, blue, and violet fell on the bridge.

The ants, however, walked backwards and forwards without (perhaps from excitement) taking any notice of the colour.

I then allowed some ants (*Lasius niger*) to find some larvæ, to which they obtained access over a narrow paper bridge. When they had got used to it, I arranged so that it passed through a dark box, and threw on it the principal colours of the spectrum, namely, red, yellow, green, blue, and violet, as well as the ultra-red and ultra-violet; but the ants took no notice.

It is obvious that these facts suggest a number of interesting inferences. I must, however, repeat the observations and make others; but we may at least, I think, conclude from the preceding that:—(1) ants have the power of distinguishing colours; (2) that they are very sensitive to violet; and it would also seem (3) that their sensations of colour must be very different from those produced upon us.

But I was anxious to go beyond this, and to attempt to determine how far their limits of vision are the same as ours. We all know that if a ray of white light is passed through a prism, it is broken up into a beautiful band of colours—the spectrum. To our eyes this spectrum is bounded by red at the one end and violet at the other, the edge being sharply marked at the red end, but less abruptly at the violet. But a ray of light contains, besides the rays visible to our eyes, others which are called, though not with absolute correctness, heat-rays and chemical-rays. These, so far from falling within the limits of our vision, extend far beyond it, the heat-rays at the red, the chemical rays at the violet end.

I have tried various experiments with spectra derived from sunlight; but, owing to the rotation of the earth, they were not thoroughly satisfactory. Mr. Spottiswoode was also good enough to enable me to make some experiments with electric light, which were not very conclusive; more recently I have made some additional and much more complete experiments, through the kindness of Professor Dewar, Professor Tyndall, and the Board of Managers of the Royal Institution, to whom I beg to offer my cordial thanks.

Of course, the space occupied by the visible spectrum is well marked off by the different colours. Beyond the visible spectrum, however, we have no such convenient landmarks, and it is not enough to describe it by inches, because so much depends on the prisms used. If, however, paper steeped in thalline is placed in the ultra-violet portion of the spectrum, it gives, with rays of a certain wave-length, a distinctly visible green colour, which therefore constitutes a green band, and gives us a definite, though rough, standard of measurement.

In the above experiments with coloured spectra, the ants carried the pupæ out of the portion of the nest on which coloured light was thrown and deposited them against the wall of the nest; or, if I arranged a nest of *Formica fusca* so that it was entirely in the light, they carried them to one side or into one corner. It seemed to me, therefore, that it would be interesting so to arrange matters, that on quitting the spectrum, after passing through a dark space, the ants should encounter not a solid obstacle, but a barrier of light. With this object, I prepared some nests 12 inches long by 6 inches wide; and Mr Cottrell kindly arranged for me at the Royal Institution on the 29th of June, by means of the electric light, two spectra, which were thrown by two glass prisms on to a table at an angle of about 45°. Each occupied about 6 inches square, and there was a space of about 2 inches between them—that is, between the red end of the one and the violet of the other.

Experiment 1.—In one of the spectra I placed a nest of *Formica fusca*, 12 inches by 6, containing about 150 pupæ, and arranged it so that one end was distinctly beyond the limit of the violet visible to us, and all but to the edge of the green given by thalline paper, and the other just beyond the visible red. The pupæ at first were almost all in or beyond the violet, but were carried into the dark space between the two spectra, the bright thalline band being avoided, but some pupæ being deposited in the red.

Experiment 2.—I then tried the same experiment with a nest of *Lasius niger*, in which there were many larvæ as well as pupæ. They were all at the commencement at the blue end of the nearer spectrum. The larvæ were left by themselves in the violet, while pupæ were ranged from the end of the green to that of the red inclusive.

Experiment 3.—Arranged a nest of *L. niger* as before; at the commencement the pupæ and larvæ were much scattered, being, however, less numerous in the violet and ultra-violet rays. Those in the ultra-violet rays were moved first, and were deposited, the larvæ in the violet, and the pupæ in the red.

Experiment 4.—Made the same experiment with another nest of *L. niger*. At the commencement the larvæ and pupæ were in the violet and ultra-violet portion, extending to double the distance from the visible end to the thalline band. The ants soon began bringing the pupæ to the red. Over part of the red I placed a piece of money. The pupæ were cleared from the ultra-violet first. That the pupæ were not put in the red for the sake of the red light was evident, because the space under the coin was even more crowded than the rest. The pupæ were heaped up in the dark as far as the thalline band of the other spectrum. I then brought the second spectrum nearer to the first. The pupæ which thus came to be in the thalline band were gradually moved into the dark.

Experiment 5.—Tried the same with another nest of *L. niger*. The pupæ were at first in the violet and ultra-violet about double as far as the thalline line, while most of the larvæ were in the green. The furthest part was cleared first; and they were again brought principally into the yellow, red, and dark.

Again, I scattered them pretty equally, some being in the ultra-violet portion, as far as double the distance of the thalline from the violet; most, however, being in the violet and blue.

The ants began by removing the pupæ which were in and near the thalline band, and carried them into the yellow or red.

Experiment 6.—Repeated the same experiment. Begun it at 11.15. Placed some pupæ in the red, some in the yellow, and a few scattered over the second spectrum; there were none in the nearer one.

They were all carried away from the red past the violet, and put down in the dark portion, or in the red and yellow, of the nearer spectrum.

These experiments surprised me much at the time, as I had expected all the pupæ to be carried into the space between the two spectra; but it afterwards occurred to me that the ultra-violet rays probably extended further than I had supposed, so that even the part which lay beyond the thalline band contained enough rays to appear light to the ants. Hence perhaps they selected the red and yellow as a lesser evil.

Experiment 7.—I altered, therefore, the arrangement. Professor Dewar kindly prepared for me a condensed pure spectrum (showing the metallic lines) with a Siemens' machine, using glass lenses and a mirror to give a perpendicular incidence when thrown on the nest. I arranged the pupæ again in the ultra-violet as far as the edge of the fluorescent light shown with thalline paper. The pupæ were all again removed, and most of them placed just beyond the red, but none in the red or yellow.

Experiment 8.—Arranged the light as before, and placed the pupæ in the ultra-violet rays. In half an hour they were all cleared away and carried into the dark space beyond the red. We then turned the nest round so that the part occupied by the pupæ again came to be in the violet and ultra-violet. The light chanced to be so arranged that along one side of the nest was a line of shadow; and into this the pupæ were carried, all those in the ultra-violet being moved. We then shifted the nest a little, so that the violet and ultra-violet fell on some of the pupæ. These were then all carried into the dark, the ones in the ultra-violet being moved first.

In these experiments with the vertical incidence there was less diffused light, and the pupæ were in no case carried into the red or yellow.

Experiment 9.—I arranged the light and the ants as before, placing the pupæ in the ultra-violet, some being distinctly beyond the bright thalline band. The ants at once began to remove them. At first many were deposited in the violet, some, however, being at once carried into the dark beyond the red. When all had been removed from the ultra-violet, they directed their attention to those in the violet, some being carried, as before, into the dark, some into the red and yellow. Again, when those in the violet had all been removed, they began on the pupæ in the red and yellow, and carried them also into the dark. This took nearly half an hour. As I had arranged the pupæ so that it might be said that they were awkwardly placed, we then turned the nest round, leaving the pupæ otherwise as they had been arranged by the ants; but the result of moving the nest was to bring some of them into the violet, though most were in the ultra-violet. They were, as before, all carried into the dark space beyond the red in about half an hour.

We then turned the glass round again, this time arranging the end about the length of the spectrum beyond the end of the violet visible to our eyes. They began clearing the thalline band, carrying some into the violet, but the majority away further from the spectrum. In a quarter of an hour the thalline band had been quite cleared; and in half an hour a band beyond, and equal to the thalline band, those in the violet being left untouched. After the pupæ in the ultra-violet portion had all been moved, those in the violet were also carried away and deposited about twice as far from the edge of the violet as the further edge of the bright thalline band.

Experiment 10.—Experimented again with the same arrangement as before, using another nest of *Lasius niger* and placing the pupæ in the violet and a little beyond. The ants at once began removing them into the dark, tunnelling into the heap, and then carrying away those in the ultra-violet first, although they were further off. In half an hour they had all been moved out of the violet and ultra-violet, about half being placed in the dark, and half having been provisionally deposited in the red and yellow.

Experiment 11.—Same arrangement as before.

The pupæ being placed all along one side of the nest, from the edge of the red to a distance beyond the violet as great as the whole length of the spectrum. I began at 4.15. By degrees they were all cleared away from the spectrum, except those in the violet, where indeed, and immediately outside of which, the others were placed. At 5, however, they began to carry them back into the red. At 5.45 the blue and violet were nearly cleared, the pupæ being placed in the red and yellow. At 6.15 they had all been brought from the violet and ultra-violet into the red and yellow.

I then shook up the pupæ so that they were arranged all along one side of the nest, and extended about an inch beyond the red. This excited the ants very much, and in less than ten minutes all those in the spectrum, and for about 6 inches beyond the violet, were moved, but at first they were put down anywhere, so that they were scattered all over the nest. This, however, lasted for a very short time and they were all carried into the dark beyond the red, or into the extreme end at some distance beyond the violet. At 7 the edge of the heap of pupæ followed the line of the red at one end, coming about $\frac{1}{4}$ inch within it, which was not owing to want of room, as one side of the nest was almost unoccupied; at the other end they were all carried 3 inches beyond the end of the violet.

It would seem, then, as the result of these experiments, that the limits of vision of ants at the red end of the spectrum are approximately the same as ours, that they are not sensitive to the ultra-red rays; but, on the other hand, that they are very sensitive to the ultra-violet rays, which our eyes cannot perceive.

I then arranged the same ants in a wooden frame consisting of a base and two side walls, between which in the middle was a perpendicular sliding door. The pupæ had been arranged by the ants in the centre of the nest, so that some were on each side of the door. We then threw, by means of a strong induction-coil, a magnesium-spark on the nest from one side, and the light from a sodium-flame in a Bunsen burner on the other, the light being in each case stopped by the sliding door, which was pressed close down on the nest. In this way the first half was illuminated by the one light, the second by the other, the apparatus being so arranged that the lights were equal to our eyes—that, however, given by the magnesium, consisting of mainly blue, violet, and ultra-violet rays, that of the sodium being very yellow and poor in chemical rays. In a quarter of an hour the pupæ were all carried into the yellow. The sodium light being the hotter of the two, to eliminate the action of heat I introduced a water-cell between the ants and the sodium-flame, and made the two sides as nearly as possible equally light to my eye. The pupæ, however, were again carried into the sodium side.

I repeated the same experiment as before, getting the magnesium-spark and the sodium-flame to the same degree of intensity, as nearly as my eye could judge, and interposing a water-screen between the sodium-flame and the ants. The temperature was tested by the thermometer, and I could distinguish no difference between the two sides. Still the ants preferred the sodium side. This I repeated twice. I then removed the magnesium-spark somewhat, so that the illumination on that side was very much fainter than on the other; still the pupæ were carried into the sodium-light. I then turned the nest round so as to bring them back into the magnesium. They were again carried to the sodium side.

Once more I repeated the same experiment. The light on the magnesium side was so faint that I could scarcely see the pupæ, those on the sodium side being quite plain. The thermometer showed no difference between the two sides. The pupæ were carried into the sodium-light. I then turned the nest round twice; but the pupæ were each time carried out of the magnesium-light.

These experiments seemed strongly to indicate, if not to prove, that ants were really sensitive to the ultra-violet rays. Now to these rays sulphate of quinine and bisulphide of carbon are extremely opaque, though perfectly transparent in the case of visible rays, and therefore to our eyes entirely colourless and transparent. If, therefore, the ants were really affected by the ultra-violet rays, then a cell containing a layer of sulphate of quinine or bisulphide of carbon would tend to darken the underlying space to their eyes, though to ours it would not do so.

It will be remembered that if an opaque substance is placed over a part of a glass nest, other things being equal, the ants always congregate under it ; and that if substances of different opacity are placed on different parts of a nest, they collect under that which seems to them most opaque. Over one of my nests of *Formica fusca*, therefore, I placed two pieces of dark-violet glass 4 inches by 2 inches ; and over one of them I placed a cell containing a layer of bisulphide of carbon, an inch thick, slightly coloured with iodine. In all these experiments, when I moved the liquids or glasses, I gave the advantage, if any, to the one under which experience showed that the ants were least likely to congregate. The ants all collected under the glass over which was the bisulphide of carbon.

I then thought that though no doubt the iodine rendered the bisulphide more completely impervious to the ultra-violet rays, I would try the effect of it when pure and perfectly colourless. I therefore tried the same experiment with pure bisulphide, moving the two glasses from time to time in such a manner that the ants had to pass the first violet glass in order to reach that over which was the bisulphide.

At 8.30 the ants were all under the glass over which was the bisulphide of carbon : I then changed the position.

8.45	,,	,,	,,
9	,,	,,	,,
9.15	,,	,,	,,

Although the bisulphide of carbon is so perfectly transparent, I then thought I would try it without the violet glass. I therefore covered part of the nest with violet glass, a part with a layer of bisulphide of carbon, moving them from time to time as before, and the ants in every case went under the bisulphide.

I then reduced the thickness of the layer of bisulphide to $\frac{4}{10}$ of an inch, but still they preferred the bisulphide.

Then thinking that possibly the one shelter being a plate of glass and the other a liquid might make a difference, I tried two similar bottles, one containing water and the other bisulphide of carbon; but in every case the ants went under the bisulphide of carbon. On the other hand, when I used coloured solutions so deep in tint that the ants were only just visible through them, the ants went under the coloured liquids.

10th October.—I uncovered the nest at 7 a.m., giving the ants an option between the bisulphide of carbon and various coloured solutions, taking for violet ammonio-sulphate of copper; for red, a solution of carmine so deep in tint that the ants could only just be seen through it; for green, a solution of chlorate of copper; and for yellow, saffron. They were each separately tried with the bisulphide, and in every case the ants preferred the coloured solution.

I now took successively red, yellow, and green glass; but in every case the ants preferred the glass to the bisulphide. Although, therefore, it would seem from the previous experiments that the bisulphide darkened the nests to the ants more than violet glass, it would appear to do so less than red, green, or yellow.

I now made some experiments in order, if possible, to determine whether the reason why the ants avoided the violet glass was because they disliked the colour violet, or whether it was because the violet glass transmitted more of the ultra-violet rays.

For this purpose I placed a layer of the bisulphide of carbon over a piece of violet glass. By this arrangement I got the violet without the ultra-violet rays; and I then contrasted this combination with other coloured media.

First, I took a solution of bichromate of potash (bright orange) and placed it on a part of the nest, side by side with the violet glass and bisulphide of carbon. I should add that the bichromate of potash also cuts off the ultra-violet rays. In all the following observations I changed the position after each observation.

At 1.30 p.m.	the ants	were	under the bichromate.
3	,,	,,	equally divided.
8 a.m.	,,	,,	under the bichromate.
8.30	,,	,,	under the violet glass and bisulphide.
9	,,	,,	equally divided.
9.30	,,	,,	some under each, but most under the violet glass and bisulphide.

9.45 the ants were equally divided.

10 ,, ,, ,,

In this case, therefore, though without the layer of bisulphide the violet glass would always have been avoided, the result of placing the bisulphide over the violet glass was that the ants did not care much whether they were under the violet glass or under the bichromate of potash.

I then took the same solution of carmine which I had already used.

10	The ants were	under the carmine.
10.15	,,	,, ,,
10.30	,,	most under the carmine, but some under the violet.
10.45	,,	under the carmine.
11	,,	most under the carmine, but some under the violet.

Here, then, again the bisulphide made a distinct difference, though not so much so as with the bichromate of potash.

I then took the solution of chlorate of copper already used.

1 The ants were equally divided.
1.30 The greater number were under the violet glass and bisulphide.
2 The greater number were under the violet glass and bisulphide.
2.30 The greater number were under the violet glass and bisulphide.
3 Almost all were under the glass and bisulphide.

The addition of the bisulphide thus caused the violet glass to be distinctly preferred to the chlorate of copper.

I then took a solution of sulphate of nickel, almost exactly the same tint as, or a shade paler than, the chlorate of copper.

At 3.45 the ants were under the violet glass and bisulphide.
4 ,, ,, ,,
5 ,, ,, ,,

18th October:
7 a.m. ,, ,, ,,
8 The ants were equally divided.

Here the effect was even more marked.

I then took some saffron 1 inch in thickness and of a deep-yellow colour.

12.45 The ants were about half under each.
1 Most of the ants were under the violet glass and bisulphide.
1.15 ,, ,, ,,
2 Most of the ants were under the saffron.

Here, again, we have the same result.

I then tried the different-coloured glasses, all of which, as I had previously found, are unmistakably preferred to the violet. It remained to be seen what effect placing the bisulphide of carbon on the violet would have.

First, I placed side by side, as usual, a piece of green glass and the violet glass covered with bisulphide of carbon:—

1st exp. The ants were equally divided.
2nd ,, They were under the violet glass and bisulphide.
3rd ,, ,, ,, ,,
4th exp. Most of them were under the violet glass and bisulphide.
5th ,, ,, ,, ,,

Next, I tried pale-yellow glass.

1st obs. The ants were almost all under the violet glass and bisulphide.
2nd ,, About three-quarters were ,, ,,
3rd ,, They were all ,, ,,
4th ,, About half were under each.

I then took the dark-yellow glass.

1st obs. About half the ants were under the yellow glass and half under the violet glass and bisulphide.
2nd ,, Most of them were under the violet glass and bisulphide.
3rd ,, ,, ,, yellow glass.
4th ,, ,, ,, violet glass and bisulphide.
5th ,, Equally divided.

I now took deep-red glass.

1st obs. The ants were under the red glass.
2nd ,, Half of the ants were under each.
3rd ,, Most of the ants were under violet glass and bisulphide.
4th ,, The ants were equally divided.

It seemed evident, therefore, that while if violet glass alone was placed side by side with red, yellow, or green, the ants greatly preferred any of the latter, on the other hand, if a layer of bisulphide of carbon, which to our eyes is perfectly transparent, was placed over the violet glass, they then went as readily, or even more readily, under it than under other colours.

In order to be sure that it was not the mere presence of a fluid, or the two layers of glass, to which this was due, I thought it would be well to try a similar series of experiments, using, however, a layer of similar thickness (1 inch) of water coloured light blue by ammonio-sulphate of copper.

I therefore took again the piece of violet glass, over which I placed a flat-sided bottle, about 1 inch thick, containing a light-blue solution of ammonio-sulphate of copper; and, in contrast with it, I used the same coloured glasses as before. The difference, however, was very marked, the ants always preferring the red, green, and yellow to the violet.

These experiments seem to demonstrate that in the previous series the ants were really influenced by some difference due to the bisulphide of carbon, which affected their eyes, though not ours.

I then thought it would be interesting to use, instead of the bisulphide, a solution of sulphate of quinine ($\frac{1}{2}$ dr. to 4 ounces), which differs from it in many points, but agrees in cutting off the ultra-violet rays. I used, as before, a layer about an inch thick, which I placed over violet glass, and then placed by its side the same coloured glasses as before.

First, I took the red glass.

Obs. 1 The ants were about equally divided.
,, 2 Most of them were under the red glass.
,, 3 Nearly equally divided; rather more under the violet glass and sulphate of quinine than under the red glass.
,, 4 ,, ,, ,,

I now took the dark-yellow glass instead of the red.

Obs. 1 Most of the ants were under the violet glass and sulphate of quinine.
,, 2 ,, ,, ,, ,,
,, 3 ,, ,, ,, ,,
,, 4 ,, ,, ,, yellow glass.
,, 5 ,, ,, ,, ,,
,, 6 All the ants were under the violet glass and sulphate of quinine.

Obs. 7 Equally divided.
,, 8 Rather more under the violet glass and sulphate of quinine than under the yellow glass.

I then took the light-yellow glass instead of the dark.

Obs. 1 The ants were all under the violet glass and sulphate of quinine.
,, 2 Rather more than half under the yellow glass.
,, 3 Almost all under the violet glass and sulphate of quinine.
,, 4 All ,, ,, ,,

I then took the green glass instead of the yellow.

Obs. 1 They were under the violet glass and sulphate of quinine.
,, 2 ,, ,, ,,
,, 3 Equally divided.
,, 4 About three-quarters under the green glass.
,, 5 Almost all under the violet glass and sulphate of quinine.

Thus, then, while if the ants have to choose between the violet and other coloured glasses, they will always prefer one of the latter, the effect of putting over the violet glass a layer either of sulphate of quinine or bisulphide of carbon, both of which are quite transparent to our eyes, but both of which cut off the ultra-violet rays, is to make the violet glass seem to the ants as good a shelter as any of the other glasses. This seems to me strong evidence that the ultra-violet rays are visible to the ants.

I then tried similar experiments with a saturated solution of chrome alum and chromium chloride. These are dark greenish-blue, very opaque to the visible light-rays, but transparent to the ultra-violet. I used a layer $\frac{1}{4}$ inch thick, which was still so dark that I could not see the ants through it; and for comparison, a solution 1 inch thick of bisulphide of carbon, moving them after each observation as before.

Exp.	1	The ants were under the bisulphide of carbon.		
,,	2	,,	,,	,,
,,	3	Most of the ants were under the bisulphide of carbon.		
,,	4	All but three	,,	,,
,,	5	All	,,	,,

I now took chromium chloride instead of alum.

Exp.	1	Most were under the bisulphide of carbon.		
,,	2	All ,,	,,	,,
,,	3	Almost all	,,	,,
,,	4	About three-fourths were under the chromium chloride.		
,,	5	All were under the chromium chloride.		
,,	6	About two-thirds		,,
,,	7	About one-half under each.		
,,	8	All under the bisulphide of carbon.		
,,	9	About three-fourths under the bisulphide of carbon.		
,,	10	About half	,,	,,
,,	11	All under the chromium chloride.		
,,	12	,, bisulphide of carbon.		

This result is very striking. It appears to show that though to our eyes the bisulphide of carbon is absolutely transparent, while the chrome alum and chromium chloride are very dark, to the ants, on the contrary, the former appears to intercept more light than a layer of the latter, which to our eyes appears dark green.

The only experiments hitherto made with the view of determining the limits of vision of animals have been some by Professor Paul Bert * on a small fresh-water crustacean belonging to the genus *Daphnia*, from which he concludes that they perceive all the colours known to us, being, however, specially sensitive to the yellow and green, and that their limits of vision are the same as ours.

Nay, he even goes further than this, and feels justified

* *Archiv. de Physiol.*, 1869, p. 547.

in concluding from the experience of two widely divergent species—Man and *Daphnia*—that the limits of vision would be the same in all cases.

His words are :—

A. "Tous les animaux voient les rayons spectraux que nous voyons."

B. "Ils ne voient aucun de ceux que nous ne voyons pas."

C. "Dans l'étendue de la région visible, les différences entre les pouvoirs éclairants des différents rayons coloriés sont les mêmes pour eux et pour nous."

He adds, that "puisque les limites de visibilités semblent être les mêmes pour les animaux et pour nous, ne trouvons-nous pas là une raison de plus pour supposer que le rôle des milieux de l'œil est tout-à-fait secondaire et que la visibilité tient à l'impressionnabilité de l'appareil nerveux lui-même ? "

Such a generalization would seem to rest on but a slight foundation ; and I may add that I have made some experiments myself * on *Daphnias* which do not agree with those of M. Bert. On the contrary, I believe that the eyes of *Daphnias* are in this respect constituted like those of ants.

These experiments seem to me very interesting. They appear to prove that ants perceive the ultra-violet rays. Now, as every ray of homogeneous light which we can perceive at all appears to us as a distinct colour, it becomes probable that these ultra-violet rays must make themselves apparent to the ants as a distinct and separate colour (of which we can form no idea), but as unlike the rest as red is from yellow, or green from violet. The question also arises whether white light to these insects would differ from our white light in containing this additional colour. At any rate, as few of the colours in nature are pure, but almost all arise from the combination of rays of different wave-lengths, and as in such cases the visible resultant would

* *British Assoc. Report*, 1881, and *Linnean Soc. Journ.*, 1882.

be composed not only of the rays which we see, but of these and the ultra-violet, it would appear that the colours of objects and the general aspect of nature must present to them a very different appearance from what it does to us.[47]

The Sense of Hearing

Many eminent observers have regarded the antennæ of insects as auditory organs, and have brought forward strong evidence in favour of their view.

I have myself made experiments on grasshoppers, which convinced me that their antennæ serve as organs of hearing.

So far, however, as Ants, Bees, and Wasps are concerned, the evidence is very conflicting. The power of hearing has indeed generally been attributed to them. Thus St Fargeau, in his *Hist. Nat. des Hyménoptères*,* thinks there can be no doubt on the subject. Bevan expresses, no doubt, the general opinion with reference to Bees, when he says that "there is good evidence that Bees have a quick sense of hearing".†

As regards Wasps, Ormerod, who studied them so lovingly, came to the same conclusion.‡

On the other hand, both Huber § and Forel || state that ants are quite deaf. As I have already mentioned in the *Linnean Journal* (vols. xii and xiii), I have never succeeded in satisfying myself that my ants, bees, or wasps heard any of the sounds with which I tried them. I have over and over again tested them with the loudest and shrillest noises I could make, using a penny pipe, a dog-whistle, a violin, as well as the most piercing and startling sounds I could produce with my own voice, but all without effect. At the same time, I carefully avoided inferring from this that they are really deaf, though it certainly seems that their range of hearing is very different from ours.

* Vol. i, p. 113.

† *The Honey Bee*, p. 264.

‡ *Nat. Hist. of Wasps*, p. 72.

§ *Nat. Hist. of Ants.*

|| *Fourmis de la Suisse*, p. 121.

In order, if possible, to throw some light upon this interesting question, I made a variety of loud noises, including those produced by a complete set of tuning-forks, as near as possible to the ants mentioned in the preceding pages, while they were on their journeys to and fro between the nests and the larvæ. In these cases the ants were moving steadily and in a most business-like manner, and any start or alteration of pace would have been at once apparent. I was never able, however, to perceive that they took the slightest notice of any of these sounds. Thinking, however, that they might perhaps be too much absorbed by the idea of the larvæ to take any notice of my interruptions, I took one or two ants at random and put them on a strip of paper, the two ends of which were supported by pins with their bases in water. The ants imprisoned under these circumstances wandered slowly backwards and forwards along the paper. As they did so, I tested them in the same manner as before, but was unable to perceive that they took the slightest notice of any sound which I was able to produce. I then took a large female of *Camponotus ligniperdus*, and tethered her on a board to a pin by a delicate silk thread about 6 inches in length. After wandering about for a while, she stood still, and I then tried her in the same way; but, like the other ants, she took no notice whatever of the sounds.

It is of course possible, if not probable, that ants, even if deaf to sounds which we hear, may hear others to which we are deaf.

Having failed, therefore, in hearing them or making them hear me, I endeavoured to ascertain whether they could hear one another.

To ascertain then if possible whether ants have the power of summoning one another by sound, I tried the following experiments. I put out (September, 1874) on the board where one of my nests of *Lasius flavus* was usually fed, six small pillars of wood about an inch and a half high, and on one of them I put some honey. A number of ants were wandering about on the board itself in search of food, and the nest itself was immediately above, and about 12 inches from, the board. I then put three ants to the honey, and when each had sufficiently fed I imprisoned her and put another; thus always keeping three ants at the honey, but not allowing them to go home. If then they could summon their friends by sound, there ought soon to be many ants at the honey. The results were as follow :—

8th September.—Began at 11 a.m. Up to 3 o'clock only seven ants found their way to the honey, while about as many ran up the other pillars. The arrival of these seven, therefore, was not more than would naturally result from the numbers running about close by. At 3 we allowed the ants then on the honey to return home. The result was that from 3.6, when the first went home, to 3.30, eleven came; from 3.30 to 4, no less than forty-three. Thus in four hours only seven came, while it was obvious that many would have wished to come, if they had known about the honey, because in the next three-quarters of an hour, when they were informed of it, fifty-four came.

On 10th September I tried the same again, keeping as before three ants always on the honey, but not allowing any to go home. From 12 to 5.30, only eight came. Those on the honey were then allowed to take the news home. From 5.30 to 6, four came; from 6 to 6.30, four; from 6.30 to 7, eight; from 7.30 to 8, no less than fifty-one.

On 23rd September we did the same again, beginning at 11.15. Up to 3.45 nine came. The ants on the honey were then allowed to go home. From 4 to 4.30 nine came; from 4.30 to 5, fifteen; from 5 to 5.30 nineteen; from 5.30 to 6, thirty-eight. Thus in three and a half hours only nine came; in two, when the ants were permitted to return, eighty-one.

Again, on 30th September I tried the same arrangement, again beginning at 11. Up to 3.30 seven ants came, We then allowed the ants which had fed to go home. From 3.30 to 4.30 twenty-eight came. From 4.30 to 5, fifty-one came. Thus in four hours and a half only seven came; while when the ants were allowed to return no less than seventy-nine came in an hour and a half. It seems obvious therefore that in these cases no communication was transmitted by sound.

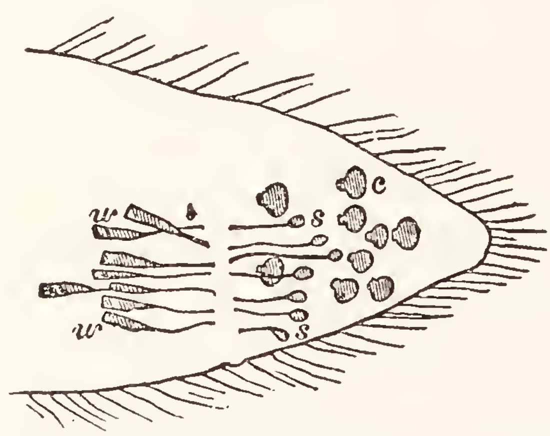
Again, Professor Tyndall was good enough to arrange for me one of his sensitive flames; but I could not perceive that it responded in any way to my ants. The experiment was not, however, very satisfactory, as I was not able to try the flame with a very active nest. Professor Bell most kindly set up for me an extremely sensitive microphone: it was attached to the underside of one of my nests; and though we could distinctly hear the ants walking about, we could not distinguish any other sound.

It is, however, far from improbable that ants may produce sounds entirely beyond our range of hearing. Indeed, it is not impossible that insects may possess senses, or sensations, of which we can no more form an idea than we should have been able to conceive red or green if the human race had been blind. The human ear is sensitive to vibrations reaching at the outside to about 38,000 in a second. The sensation of red is produced when 470 millions of millions of vibrations enter the eye in a similar time; but between these two numbers, vibrations produce on us only the sensation of heat; we have no special organs of sense adapted to them. There is, however, no reason in the nature of things why this should be the case with other animals; and the problematical organs possessed by many of the lower forms may have relation to sensations which we do not perceive. If any apparatus could be devised by which the number of vibrations produced by any given cause could be lowered so as to be brought within the range of our ears, it is probable that the result would be most interesting.

Moreover, there are not wanting observations which certainly seem to indicate that ants possess some sense of hearing.

I am, for instance, indebted to Mr Francis Galton for the following quotation from Colonel Long's recent work on Central Africa.* "I observed," he says, "the manner of catching them" (the ants, for food), "as here pictured" (he gives a figure). "Seated round an ant-hole were two very pretty maidens, who with sticks beat upon an inverted gourd, "bourmah," in cadenced time to a not unmusical song, that seduced from its hole the unwary ant, who, approaching the orifice, was quickly seized." The species of ant is not mentioned.[48]

Fig. 6.



Terminal portion of antenna of *Myrmica ruginodis* ☿ × 75.

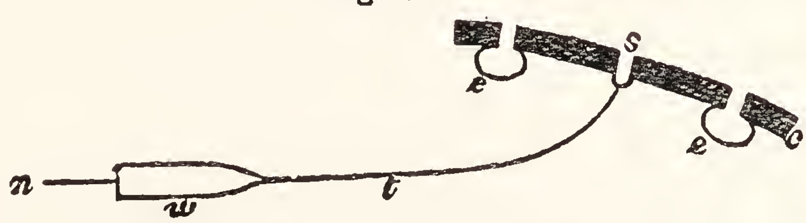
Moreover, there are in the antennæ certain remarkable structures, which may very probably be auditory organs. These curious organs (Fig. 6) were first noticed, so far as I am aware, by Dr J. Braxton Hicks in his excellent paper on the "Antennæ of Insects", published in the 22nd volume of the *Linnæan Transactions* †; and, again, by Dr Forel in his *Fourmis de la Suisse*. They certainly deserve more attention than they have yet received. The cork-shaped organs (Figs. 6 and 7, *e e*) occur in allied species; but these stethoscope-like organs have not, so far as I am aware, been yet observed in other insects.

* *Central Africa*, by Col. C. C. Long, p. 274.
† *Trans. of Linnæan Soc.*, vol. xxii, p. 391.

They consist of an outer sac (Figs. 6 and 7, *s*), of a long tube (*t*), and a posterior chamber (*w*), to which is given a nerve (*n*).

Forel * also describes these curious organs. He appears to consider that the number varies considerably, namely, from 5 to 12. My own impression is that this difference is only apparent, and that in reality the numbers in each species vary little. Though sometimes the presence of air renders them very conspicuous, they are in others by no means easy to make out; and I think that when a small number only are apparently present, this is probably due merely to the fact that the others are not brought out by the mode of preparation.

Fig. 7.



Diagrammatic section through part of Fig. 6.

c, chitinous skin of the antenna. *e e*, two of the cork-shaped organs. *s*, external chamber of one of the stethoscope-shaped organs. *t*, the tube. *w*, the posterior sac. *n*, the nerve.

In addition to the group of these organs situated in the terminal segment, there is one, or in some rare cases I have found two, in each of the small preceding segments. The tubes in these segments appeared to the eye to be nearly of the same length as those in the terminal segment, but I could not measure their exact length, as they do not lie flat. In some cases, when the segment was short, the tube was bent—an indication perhaps, that the exact length is of importance. It is possible that these curious organs may be auditory, and serve like microscope stethoscopes. Professor Tyndall, who was good enough to examine them with me, concurred in the opinion that this was very probable. I believe I am

* *Fourmis de la Suisse*, p. 301.

correct in saying that the bending of the tube in the short segments would make little difference in its mode of action.

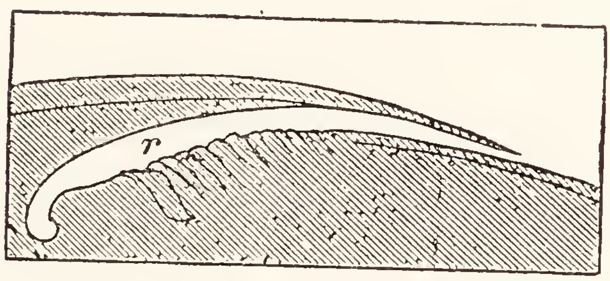
Kirby and Spence were, I believe, the first to notice that an insect allied [49] to the ants (*Mutilla europæa*) has the power of making a sibilant, chirping sound, but they did not ascertain how this was effected. Goureau * subsequently called attention to the same fact, and attributed it to friction of the base of the third segment of the abdomen against the second. Westwood,† on the other hand, thought the sound was produced "by the action of the large collar against the front of the mesothorax". Darwin, in his *Descent of Man*, adopts the same view. "I find," he says,‡ "that these surfaces (i.e. the overlapping portions of the second and third abdominal segments) are marked with very fine concentric ridges, but so is the projecting thoracic collar, on which the head articulates; and this collar, when scratched with the point of a needle, emits the proper sound." Landois, after referring to this opinion, expresses himself strongly in opposition to it. The true organ of sound is, he maintains,§ a triangular field on the upper surface of the fourth abdominal ring, which is finely ribbed, and which, when rubbed, emits a stridulating sound. It certainly would appear, from Landois' observations, that this structure does produce sound, whether or not we consider that the friction of the collar against the mesothorax may also assist in doing so.

Under these circumstances, Landois asked himself whether other genera allied to Mutilla might not possess a similar organ, and also have the power of producing sound. He first examined the genus Ponera, which, in the structure of its abdomen, nearly resembles Mutilla, and here also he found a fully developed stridulating apparatus.

* *Ann. de la Soc. Ent. de France*, 1837.
† *Modern Classification of Insects*, vol. ii.
‡ *Descent of Man*, vol. i, p. 366.
§ *Thierstimmen*, p. 132.

He then turned to the true ants,* and here also he found a similar rasp-like organ in the same situation. It is indeed true that ants produce no sounds which are audible by us; still, when we find that certain allied insects do produce sounds appreciable to us by rubbing the abdominal segments one over the other; and when we find, in some ants, a nearly similar structure, it certainly seems not unreasonable to conclude that these latter also do produce sounds, even though we cannot hear them. Landois describes the structure on the workers of *Lasius fuliginosus* as having twenty ribs in a breadth of 0·13 of a millimetre, but he gives no figure. In Fig. 8

Fig. 8.



Attachment of abdominal segments of *Lasius flavis* ☿ × 225.

I have represented the junction of the second and third abdominal segments in *Lasius flavus*, × 225, as shown in a longitudinal and vertical section. There are about ten well-marked ribs (*r*), occupying a length of approximately $\frac{1}{100}$ of an inch. Similar ridges also occur between the following segments.†

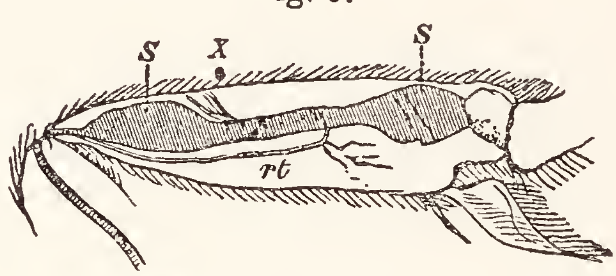
In connection with the sense of hearing I may mention another very interesting structure. In the year 1844, Von Siebold described ‡ a remarkable organ which he had discovered in the tibiæ of the front legs of *Gryllus*, and which he considered to serve for the purpose of

* Some tropical ants are said to produce a chirping sound.
† See also Sharp, *Trans. Ent. Soc.*, 1893.
‡ *Ueber das Stimm. und Gehörorgan der Orthopteren, Wiegmann's Art. f. Natur.*, 1844.

hearing. These organs have also been studied by Burmeister, Brunner, Hensen, Leydig, and others, and have recently been the subject of a monograph by Dr V. Graber,* who commences his memoir by observing that they are organs of an entirely unique character, and that nothing corresponding to them occurs in any other insects, or indeed in any other Arthropods.

I have therefore been very much interested by discovering (1875) in ants a structure which seems in some remarkable points to resemble that of the Orthoptera. As will be seen from a glance at Dr Graber's memoir, and the plates which accompany it, the large trachea of the leg in the Orthoptera is considerably swollen in the tibia, and sends off, shortly after entering the tibia,

Fig. 9.



Tibia of *Lasius flavus* ☿ × 75.

a branch which, after running for some time parallel to the principal trunk, joins it again. See, for instance, in his monograph, plate ii, fig. 43; plate vi, fig. 69; plate vii, fig. 77; etc.

Now, I have observed that in many other insects the tracheæ of the tibia are dilated, and in several I have been able to detect a recurrent branch. The same is also the case in some mites. I will, however, reserve what I have to say on this subject, with reference to other insects, for another occasion, and will at present confine myself to the ants. If we examine the tibia, say of *Lasius flavus*, Fig. 9, we shall see that the trachea presents a remarkable arrangement, which at once

* *Die Tympanalen Sinnesapparate der Orthopteren*, von Dr Vitus Graber, 1875.

reminds us of that which occurs in Gryllus and other Orthoptera. In the femur it has a diameter of about $\frac{1}{3000}$ of an inch; as soon, however, as it enters the tibia, it swells to a diameter of about $\frac{1}{500}$ of an inch, then contracts again to $\frac{1}{800}$, and then again, at the apical extremity of the tibia, once more expands to $\frac{1}{500}$. Moreover, as in *Gryllus*, so also in *Formica*, a small branch rises from the upper sac, runs almost straight down the tibia, and falls again into the main trachea just above the lower sac.

The remarkable sacs (Fig. 9, *s s*) at the two extremities of the trachea in the tibia may also be well seen in other transparent species, such, for instance, as *Myrmica ruginodis* and *Pheidole megacephala*.

At the place where the upper tracheal sac contracts (Fig. 9), there is, moreover, a conical striated organ (*x*), which is situated at the back of the leg, just at the apical end of the upper tracheal sac. The broad base lies against the external wall of the leg, and the fibres converge inwards. In some cases I thought I could perceive indications of bright rods, but I was never able to make them out very clearly. This also reminds us of a curious structure which is found in the tibiæ of Locustidæ, between the trachea, the nerve, and the outer wall, and which is well shown in some of Dr Graber's figures.

On the whole, then, though the subject is still involved in doubt, I am disposed to think that ants perceive sounds which we cannot hear.[50]

The Sense of Smell

I have also made a number of experiments on the power of smell possessed by ants. I dipped camel's-hair brushes into peppermint-water, essence of cloves, lavender-water, and other strong scents, and suspended them about $\frac{1}{4}$ of an inch above the strips of paper along which the ants were passing, in the experiments above recorded. Under these circumstances, while some of the ants passed on without taking any notice, others stopped when they came close to the pencil, and, evidently perceiving the smell, turned back. Soon, however, they returned and passed the scented pencil. After doing this two or three times, they generally took no further notice of the scent. This experiment left no doubt on my mind; still, to make the matter even more clear, I experimented with ants placed on an isolated strip of paper. Over the paper, and at such a distance as almost, but not quite, to touch any ant which passed under it, I again suspended a camel's-hair brush, dipped in assafœtida, lavender-water, peppermint-water, essence of cloves, and other scents. In this experiment the results were very marked; and no one who watched the behaviour of the ants under these circumstances could have the slightest doubt as to their power of smell.

I then took a large female of *Camponotus ligniperdus* and tethered her on a board by a thread as before. When she was quite quiet I tried her with the tuning-forks; but they did not disturb her in the least. I then approached the feather of a pen very quietly, so as almost to touch first one and then the other of the antennæ, which, however, did not move. I then dipped the pen in essence of musk and did the same; the antenna was slowly retracted and drawn quite back. I then repeated the same with the other antenna. If I touched the antenna, the ant started away, apparently smarting. I repeated the same with essence of lavender, and with a second ant. The result was the same.

Many of my other experiments—for instance, some of those recorded in the next chapter—point to the same conclusion; and, in fact, there can be no doubt whatever that in ants the sense of smell is highly developed.[51]

CHAPTER IX

GENERAL INTELLIGENCE AND POWER OF FINDING THEIR WAY

A NUMBER of interesting anecdotes are on record as to the ingenuity displayed by ants under certain circumstances.

M. Lund, for instance, tells the following story as bearing on the intelligence of ants * :—

"Passant un jour près d'un arbre presque isolé, je fus surpris d'entendre, par un temps calme, des feuilles qui tombaient comme de la pluie. Ce qui augmenta mon étonnement, c'est que les feuilles détachées avaient leur couleur naturelle, et que l'arbre semblait jouir de toute sa vigueur. Je m'approchai pour trouver l'explication de ce phénomène, et je vis qu'à peu près sur chaque pétiole était postée une fourmi qui travaillait de toute sa force; le pétiole était bientôt coupé et la feuille tombait par terre. Une autre scène se passait au pied de l'arbre: la terre était couverte de fourmis occupées à découper les feuilles à mesure qu'elles tombaient, et les morceaux étaient sur le champ transportés dans le nid. En moins d'une heure le grand œuvre s'accomplit sous mes yeux, et l'arbre resta entièrement dépouillé."

Bates † gives an apparently similar, but really very different account. "The Saüba ants," he says, "mount the tree in multitudes, the individuals being all worker-minors. Each one places itself on the surface of a leaf, and cuts with its sharp scissor-like jaws a nearly semi-circular incision on the upper side; it then takes the edge between its jaws, and by a sharp jerk detaches the piece. Sometimes they let the leaf drop to the ground,

* *Ann. des Sci. Nat.*, 1831, p. 112.
† *Naturalist on the Amazons*, vol. i, p. 26.

where a little heap accumulates, until carried off by another relay of workers ; but, generally, each marches off with the piece it has operated upon."

Dr Kerner recounts * the following story communicated to him by Dr Gredler of Botzen :—

"One of his colleagues at Innsbrück, says that gentleman, had for months been in the habit of sprinkling pounded sugar on the sill of his window, for a train of ants, which passed in constant procession from the garden to the window. One day, he took it into his head to put the pounded sugar into a vessel, which he fastened with a string to the transom of the window ; and, in order that his long-petted insects might have information of the supply suspended above, a number of the same set of ants were placed with the sugar in the vessel. These busy creatures forthwith seized on the particles of sugar, and soon discovering the only way open to them, viz. up the string, over the transom and down the window-frame, rejoined their fellows on the sill, whence they could resume the old route down the steep wall into the garden. Before long the route over the new track from the sill to the sugar, by the window-frame, transom, and string was completely established ; and so passed a day or two without anything new. Then one morning it was noticed that the ants were stopping at their old place, that is, the window-sill, and getting sugar there. Not a single individual any longer traversed the path that led thence to the sugar above. This was not because the store above had been exhausted ; but because some dozen little fellows were working away vigorously and incessantly up aloft in the vessel, dragging the sugar crumbs to its edge, and throwing them down to their comrades below on the sill, a sill which with their limited range of vision they could not possibly see ! "

Leuckart also made a similar experiment. Round a tree which was frequented by ants, he spread a band

* *Flowers and their Unbidden Guests*, Dr A. Kerner. Trans. by W. Ogle, 1878, p. 21.

soaked in tobacco water. The ants above the band after awhile let themselves drop to the ground, but the ascending ants were long baffled. At length he saw them coming back, each with a pellet of earth in its mouth, and thus they constructed a road for themselves, over which they streamed up the tree.

Dr Büchner records the following instance on the authority of a friend (M. Theuerkauf) :—

"A maple tree standing on the ground of the manufacturer, Vollbaum, of Elbing (now of Dantzic) swarmed with aphides and ants. In order to check the mischief, the proprietor smeared about a foot width of the ground round the tree with tar. The first ants who wanted to cross naturally stuck fast. But what did the next? They turned back to the tree and carried down aphides, which they stuck down on the tar one after another until they had made a bridge, over which they could cross the tar-ring without danger. The above-named merchant, Vollbaum, is the guarantor of this story, which I received from his own mouth on the very spot whereat it occurred." *

In this case I confess I have my doubts as to the interpretation of the fact. Is it not possible that as the ants descended the tree, carrying the aphides, the latter naturally stuck to the tar, and would certainly be left there. In the same way I have seen hundreds of bits of earth deposited on the honey with which I fed my ants.

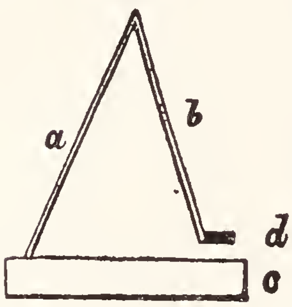
On one occasion Belt observed † a community of leaf-cutting ants (*Atta*), which was in the process of moving from one nest to another. "Between the old burrows and the new one was a steep slope. Instead of descending this with their burdens, they cast them down on the top of the slope, whence they rolled to the bottom, where another relay of labourers picked them up and carried them to the new burrow. It was amusing to watch the ants hurrying out with bundles of food, dropping them over the slope, and rushing back immediately for more." [52]

* *Mind in Animals*, by Professor Ludwig Büchner, p. 120.
† *Naturalist in Nicaragua*, O. Belt, p. 76.

With reference to these interesting statements, I tried the following experiment :—

15th October (see Fig. 10).—At a distance of 10 inches from the door of a nest of *Lasius niger* I fixed an upright ash wand 3 ft. 6 in. high (*a*), and from the top of it I suspended a second, rather shorter wand (*b*). To the lower end of this second wand, which hung just over the entrance to the nest (*c*), I fastened a flat glass cell (*d*) in which I placed a number of larvæ, and to them I put three or four specimens of *L. niger*. The drop from the glass cell to the upper part of the frame was only half an inch ; still, though the ants reached over and showed a great anxiety to take this short cut home, they none of them faced the leap, but all went round by the sticks, a distance of nearly 7 feet. At 6 p.m. there were over 550 larvæ in the glass cell, and I reduced its distance from the upper surface of the nest to about $\frac{2}{5}$ of an inch, so that the ants could even touch the glass with their antennæ, but could not reach up nor step down. Still, though the drop was so small, they all went round. At 11 p.m. the greater number of the larvæ had been carried off, so I put a fresh lot in the cell. The ants were busily at work. Next morning at 3 a.m. I visited them again. They were still carrying off the larvæ, and all going round. At 6 a.m. the larvæ were all removed. I put a fresh lot, and up to 9 a.m. they went on as before.

Fig. 10.



The following day (17th October) I took two longer sticks each 6 ft. 6 in. in length, and arranged them in a similar manner, only horizontally instead of vertically. I also placed fine earth under the glass supporting the larvæ. At 8 o'clock I placed an ant on the larvæ ; she took one, and I then coaxed her home along the sticks. She deposited her larva and immediately came out again, not, however, going along the stick, but under the larvæ, vainly reaching up and endeavouring to reach the glass. At 8.30 I put her on the larvæ again, and as she evidently did not know her way home, but kept stretching herself down and trying to reach the earth under the glass cell, I again coaxed her home along the sticks. At 9.3 she came out again, and again went under the larvæ and wandered about there. At 10 I put her on the larvæ and again helped her home. At 10.15 she came out again, and this time went to the stick, but still wanted some guidance. At 10.45 she again reached the frame, but immediately came out again, and I once more coaxed her round. After wandering about some time with a larva in her jaws, she dropped down at 11.14. After depositing her larva, she came out directly and went under the larvæ. I again coaxed her round, and this time also she dropped off the glass with her larva. At 12.30 she came out again, and for the last time I helped her round. After this she found her way by herself. At 12.20 another (No. 2) found her way round and returned at 12.37. For the next hour their times were as follows :—

No. 1.	No. 2.
12.46	
	12.47
12.54	12.54
	1. 0
1. 1	
1. 7	
	1. 8
1.12	
	1.14
1.19	
	1.21
1.26	
	1.28
1.32	
	1.34
1.38	
	1.41

No. 1.	No. 2.
1.45	
	1.47
1.52	
	1.54

Thus they both made nine visits in an hour. As regards actual pace, I found they both did about 6 feet in a minute. Soon after these began, other ants came with them. It was a beautiful day, and all my ants were unusually active. A 1 p.m. I counted 10 on the sticks at once, by 1.30 over 30, and at 5 in the afternoon over 60. They went on working very hard, and forming a continuous stream till I went to bed at 11; and at 4 in the morning I found them still at work; but though they were very anxious and, especially at first, tried very hard to save themselves the trouble of going round, they did not think of jumping down, nor did they throw the larvæ over the edge.

Moreover, as I had placed some sifted mould under the glass, a minute's labour would have been sufficient to heap up one or two particles, and thus make a little mound which would have enabled them to get up and down without going round. A mound $\frac{1}{8}$ inch high would have been sufficient; but it did not occur to them to form one.

The following morning (18th October) I put out some larvæ again at 6 a.m. Some of the ants soon came; and the same scene continued till 11.30 a.m., when I left off observing.

Again, on 22nd October, I placed a few larvæ in a glass, which I kept continually replenished, which was suspended $\frac{1}{3}$ of an inch above the surface of the frame containing their nest, but only connected with it by tapes five feet long. I then, at 6.30, put a *L. niger* to the larvæ; she took one, and tried hard to reach down, but could not do so, and would not jump; so I coaxed her round the tapes. She went into the nest, deposited her larva, and immediately came out again. I put her back on the larvæ at 7.15; she took one, and again tried hard, but ineffectually, to reach down. I therefore again coaxed her round. She went into the nest, deposited her larva, and came out again directly as before. I put her back on the larvæ at 7.35, when the same thing happened again. She got back to the nest at 7.40, and immediately came out again. This time she found her way round the string, with some help from me, and reached the larvæ at 7.50. I helped her home for the last time. The next journey she found her way without assistance, and reached the larvæ at 8.26. After this she returned as follows, viz:—

At 8.50
9. 0
9.10
9.17
9.28

I now made the length of the journey round the tapes 10 feet. This puzzled her a little at first.

She returned as follows:—

9.41	10.35
9.55	10.44
10. 8	10.54
10.16	11. 6
10.26	11.14 with a friend.

I now increased the length to 16 feet, and watched her while she made thirty journeys backwards and forwards. She also brought during the time seven friends with her.

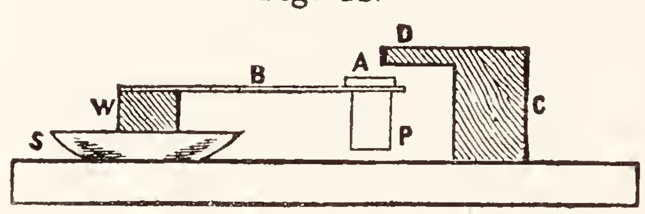
It surprised me very much that she preferred to go so far round rather than to face so short a drop.

In illustration of the same curious fact, I several times put specimens of *L. niger* on slips of glass raised only one-third of an inch from the surface of the nest. They remained sometimes three or four hours running about on the glass, and at last seemed to drop off accidentally.

Myrmica ruginodis has the same feeling. One morning, for instance, I placed one in an isolated position, but so that she could escape by dropping one-third of an inch. Nevertheless at the same hour on the following morning she was still in captivity, having remained out twenty-four hours rather than let herself down this little distance.

Again I filled a saucer (woodcut, Fig. 11, S) with water and put in it a block of wood (W), on the top of which I fastened a projecting wooden rod (B), on the end of which I placed a shallow glass cell (A) containing several hundred larvæ. From this cell I allowed a slip of paper (P) to hang down to within $\frac{3}{10}$ of an inch of the upper surface of the nest. At one side I put

Fig. 11.



another block of wood (C) with a lateral projection (D) which hung over the cell containing the larvæ. I then made a connection between D and A, so that ants could ascend C, and, passing over D, descend upon the larvæ. I then put some specimens of *Lasius niger* to the larvæ, and soon a large number of ants were engaged in carrying off the larvæ. When this had continued for about three hours, I raised D $\frac{3}{10}$ of an inch above A. The ants kept on coming and tried hard to reach down from D to A, which was only just out of their reach. Two or three, in leaning over, lost their foothold and dropped into the larvæ; but this was obviously an accident; and after a while they all gave up their efforts, and went away, losing their prize, in spite of most earnest efforts, rather than drop $\frac{3}{10}$ of an inch.

At the moment when the separation was made there were fifteen ants on the larvæ. These could, of course, have returned if one had stood still and allowed the others to get on its back. This, however, did not occur to them; nor did they think of letting themselves drop from the bottom of the paper on to the nest. Two or three, indeed, fell down, I have no doubt, by accident; but the remainder wandered about, until at length most of them got into the water. After a time the others abandoned altogether as hopeless the attempt to get at the larvæ.

I waited about six hours, and then again placed the glass (A) containing the larvæ so as to touch the piece of wood (D), and again put some ants to the larvæ. Soon a regular string of ants was established; when I again raised the wood (D) $\frac{3}{10}$ of an inch above the glass (A), exactly the same result occurred. The ants bent over and made every effort to reach the larvæ, but did not drop themselves down, and after a while again abandoned all hope of getting the larvæ.

In order to test their intelligence, it has always seemed to me that there was no better way than to ascertain some object which they would clearly desire, and then to interpose some obstacle which a little ingenuity would enable them to overcome. Following up, then, the preceding observations, I placed some larvæ in a cup which I put on a slip of glass surrounded by water, but accessible to the ants by one pathway in which was a bridge consisting of a strip of paper $\frac{2}{3}$ inch long and $\frac{1}{3}$ inch wide. Having then put a *Lasius niger* from one of my nests to these larvæ, she began carrying them off, and by degrees a number of friends came to help her. I then, when about twenty-five ants were so engaged, moved the little paper bridge slightly, so as to leave a chasm, just so wide that the ants could not reach across. They came and tried hard to do so; but it did not occur to them to push the paper bridge, though the distance was only about $\frac{1}{3}$ inch, and they might easily have done so. After trying for about a quarter of an hour, they gave up the attempt and returned home. This I repeated several times.

Then, thinking that paper was a substance to which they were not accustomed, I tried the same with a bit of straw 1 inch long and $\frac{1}{8}$ inch wide. The result was the same. I repeated this more than once.

Again, I suspended some honey over a nest of *Lasius flavus* at a height of about $\frac{1}{2}$ an inch, and accessible only by a paper bridge more than 10 feet long. Under the glass I then placed a small heap of earth. The ants soon swarmed over the earth on to the glass, and began feeding on the honey. I then removed a little of the earth, so that there was an interval of about $\frac{1}{3}$ of an inch between the glass and the earth; but, though the distance was so small, they would not jump down, but preferred to go round by the long bridge. They tried in vain to stretch up from the earth to the glass, which, however, was just out of their reach, though they could touch it with their antennæ; but it did not occur to them to heap the earth up a little, though if they had moved only half a dozen particles of earth they would have secured for themselves direct access to the food. This, however, never occurred to them. At length they gave up all attempts to reach up to the glass and went round by the paper bridge. I left the arrangement for several weeks, but they continued to go round by the long paper bridge.

Again I varied the experiment as follows: Having left a nest without food for a short time, I placed some honey on a small wooden brick surrounded by a little moat of glycerine $\frac{1}{2}$ an inch wide and about $\frac{1}{10}$ of an inch in depth. Over this moat I then placed a paper bridge, one end of which rested on some fine mould. I then put an ant to the honey, and soon a little crowd was collected round it. I then removed the paper bridge; the ants could not cross the glycerine; they came to the edge and walked round and round, but were unable to get across, nor did it occur to them to make a bridge or bank across the glycerine with the mould which I had placed so conveniently for them. I was the more surprised at this on account of the ingenuity with which they avail themselves of earth for constructing their nests. For instance, wishing, if possible, to avoid the trouble of frequently moistening the earth in my nests, I supplied one of my communities of *Lasius flavus* with a frame containing, instead of earth, a piece of linen, one portion of which projected beyond the frame and was immersed in water. The linen then sucked up the water by capillary attraction, and thus the air in the frame was kept moist. The ants approved of the arrangement, and took up their quarters in the frame. To minimize evaporation I usually closed the frames all round, leaving only one or two small openings for the ants, but in this case I left the outer side of the frame open. The ants, however, did not like being thus exposed; they therefore brought earth from some little distance, and built up a regular wall along the open side, blocking up the space between the upper and lower plates of glass, and leaving only one or two small openings for themselves. This struck me as very ingenious. The same expedient was, moveover, repeated under similar circumstances by the slaves belonging to my nest of *Polyergus*.

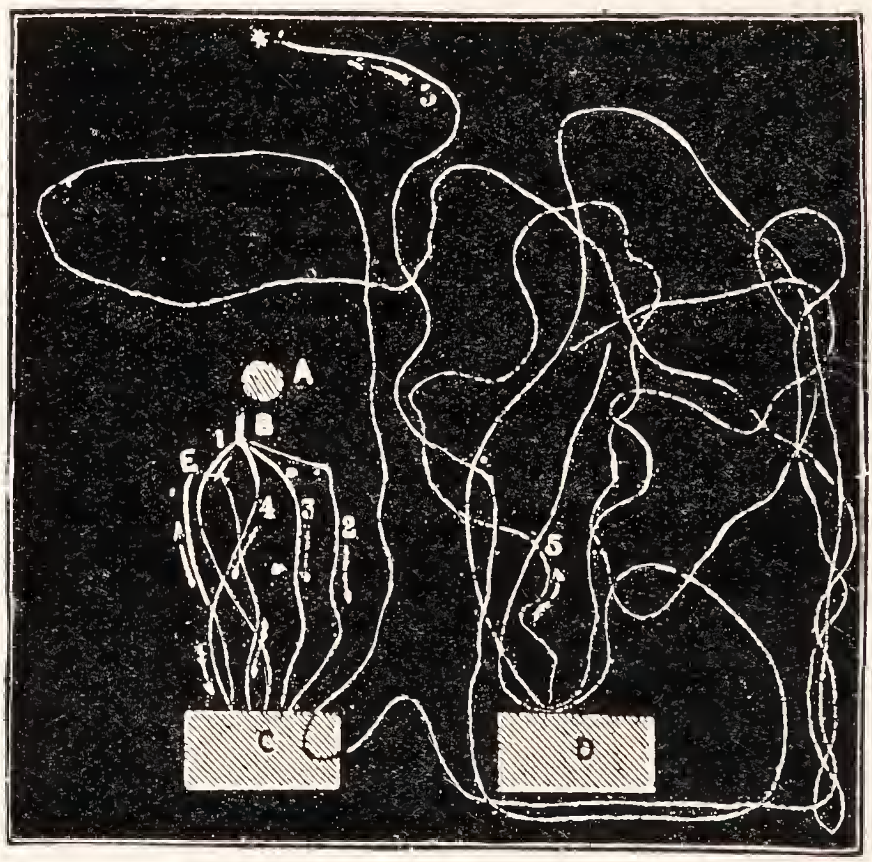
The facility or difficulty with which ants find their way, while it partly falls within the section of the subject dealing with their organs of sense, is also closely connected with the question of their general intelligence.[53]

Partly, then, in order to test how far they are guided by sight, partly to test their intelligence, I made various observations and experiments, the accompanying wood-cuts being reduced copies of tracings of some of the routes followed by the ants during the course of the observations.

I may here note that the diagrams Figs. 12–17 are careful reductions of large tracings made during the experiments. Though not absolutely correct in every minute detail of contour, they are exact for all practical purposes. As the ants pursued their way, pencil-markings in certain instances, and coloured lines in others, were made so as to follow consecutively the paths pursued.

Experiment 1.—February. On a table communicating with one of my nests (see Fig. 12) I placed upright a common cylindrical lead pencil $\frac{1}{4}$ inch in diameter

Fig. 12.

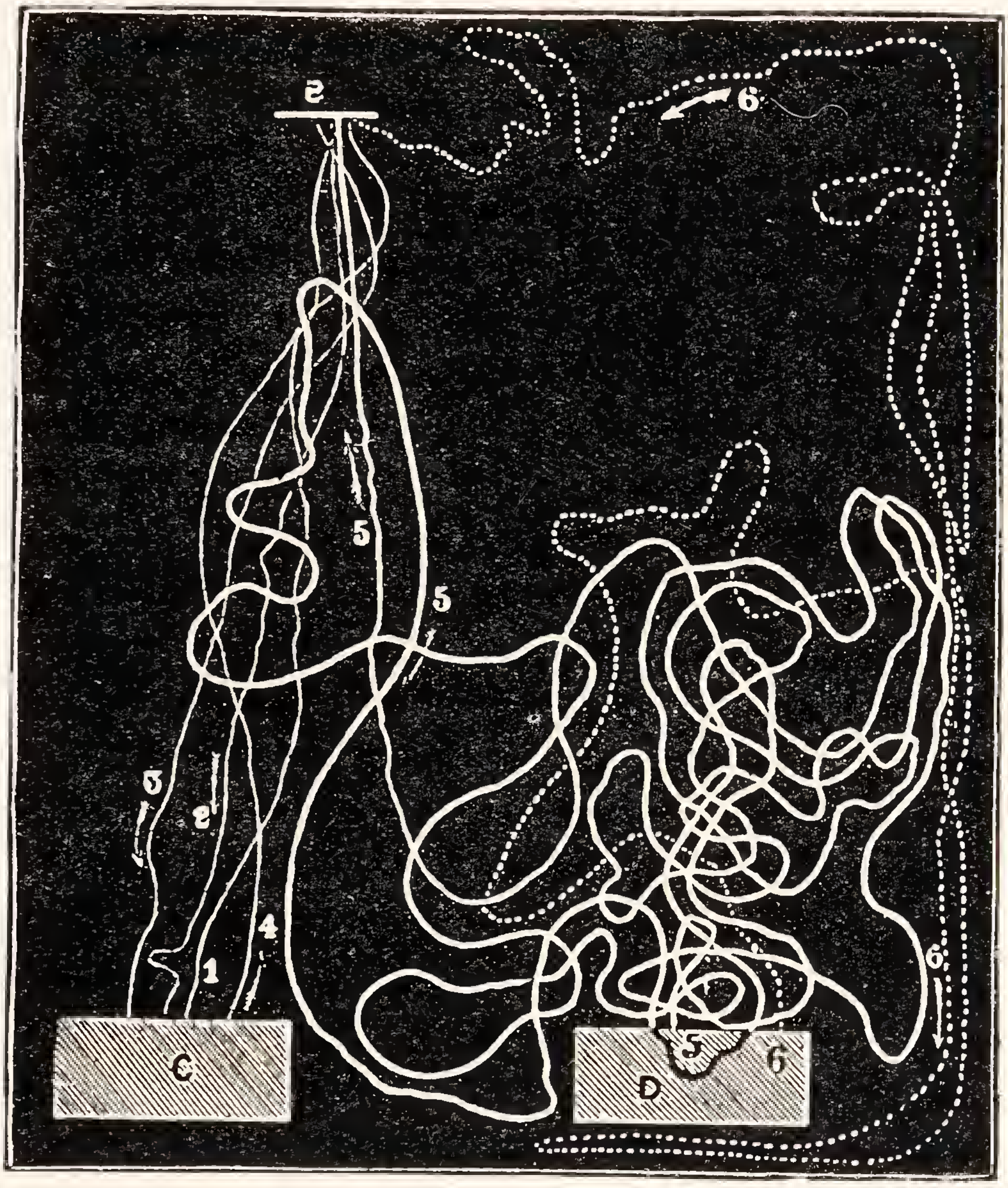


Routes followed in experiment No. 1 as detailed above.

A, position of pencil. B, paper bridge. C and D, glass with larvæ. E, point where larva dropped, the opposite arrow and loop marking return route. 1, 2, 3, 4, comparatively straight paths to the glass. 5, 5, circuitous route on shifting of glass. * different access to nest.

and 7 inches long, fastened with sealing-wax to a penny piece. Close to the base of the pencil (A) I brought the end of a paper bridge (B) leading to the nest, and then placed a shallow glass with larvæ at C, 4 inches from the base of the pencil. I then put an ant to the larvæ; when she had become acquainted with the road, she went very straight, as is shown in the woodcut (Fig. 12). In one case, at the point E, she dropped her larva and returned for another. When she returned on the next journey and was on the glass, I moved it 3 inches, to D, so that the

Fig. 13.



Routes followed in experiment No. 2, as mentioned in text.

B, paper bridge leading to nest. C, glass tray with larvæ, in its first position; and D in its position when shifted. 1, 2, 3, 4, thin white lines indicating the comparatively straight routes. 5, thick white line, and 6, dotted line showing tortuous paths when glass had been altered in position. The arrows indicate directions travelled.

end of the glass was 6 inches from the base of the pencil. If she were much guided by sight, then she would have had little or no difficulty in finding her way back. Her pathway, however (No. 5), which is traced on the paper, shows that she was completely abroad; and, after all, she got back to the nest by a different route.

I then varied the experiment as subjoined, and as shown in the wood-cut (Fig. 13).

Experiment 2.—I connected the table with the nest by a paper bridge, the end of which is shown at B (Fig. 13), and which came down about an inch from the pole supporting the nest (see Fig. 1). This pole rose 18 inches above the table. I then put the glass tray (C) with larvæ as before, 12 inches from the base of the pole, and put an ant to the larvæ. When she had learnt her way I traced four of her routes, as shown by the thin lines 1, 2, 3, 4. I then on her next journey (5, thick white line), when she was on the tray (C), moved it three inches to D, as shown in the figure, and again traced her route. The contrast is very striking between the relatively straight thin white lines 1, 2, 3, 4 of the four journeys when familar with the road; whereas in the broad white line No. 5 the zigzag twistings show how much difficulty the ant experienced in finding her way. When she returned I again moved the tray as before, and the dotted sinuous white line (6) shows the course she followed.

Experiment 3.—I then again varied the experiment as follows: I placed the larvæ in a small china cup on the top of the pencil, which thus formed a column $7\frac{1}{2}$ inches high. The cross line close to the arrows (Fig. 14) is as before, the base of the paper bridge leading to the nest. C shows the position of the penny on which the pencil was supported. The dotted white lines 1, 2, 3, 4 show the routes of a marked ant on four successive journeys from the nest to the base of the pencil. I then moved the pencil 6 inches to D, and the two following routes are marked 5 and 6. In one of them, 5 (thick white line), the ant found a stray larva at E, with which she returned to the nest, without finding the pencil at all. On the following journey, shown in the fine white zigzag

PLATE III

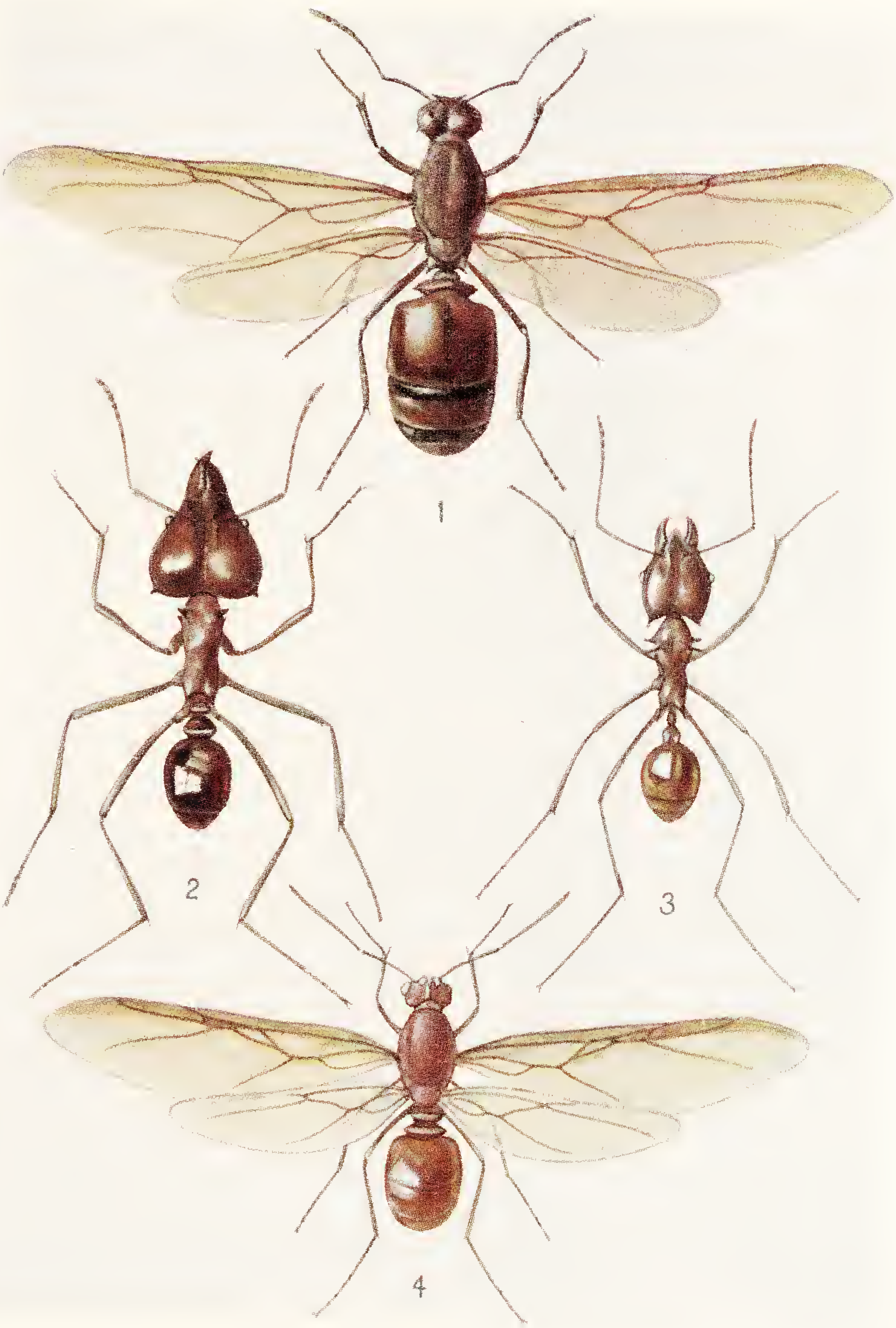


Fig. 1. *Atta cephalotes*, female. A neotropical leaf-cutting ant ($\times 1\frac{1}{2}$)

„ 2. *Atta cephalotes*, large worker ($\times 2\frac{1}{2}$)

„ 3. „ „ small worker ($\times 4$)

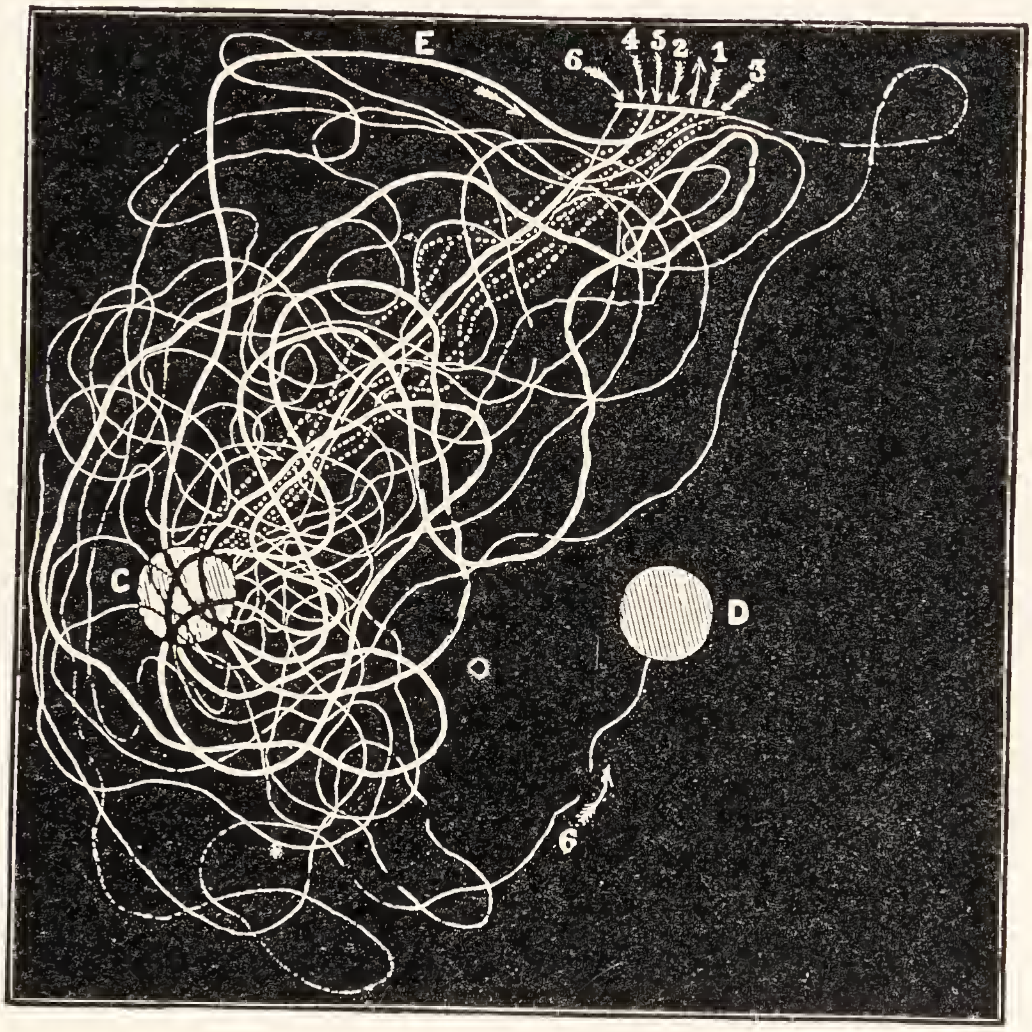
„ 4. „ „ male ($\times 1\frac{1}{2}$)

[*face p.* 192

line (6), she found the pencil at last, but, as will be seen, only after many meanderings.

Experiment 4.—I then repeated the observation on three other ants (see Figs. 15–17) with the same result: the second was 7 minutes before she found the

Fig. 14.



Routes followed in experiment No. 3, as described in text.

The line at the six arrows represents a paper bridge going to nest. C, china cup on top of pencil. D, pencil moved. E, place where a stray larva was found. 1, 2, 3, 4, dotted lines show the nearly direct journeys. 5, thick white line (crossing C in black) or route returning to nest, the ant having picked up a stray larva at E. 6, very circuitous thin white line of track from nest to pencil D.

pencil, and at last seemed to do so accidentally; the third actually wandered about for no less than half an hour (Fig. 15), returning up the paper bridge several times.

Other experiments somewhat similar to the preceding, the results of which are shown in the figures 16 and 17, seem to prove that this species of ant, at any rate, guides itself but little by sight. This which I had not at all

Fig. 15.

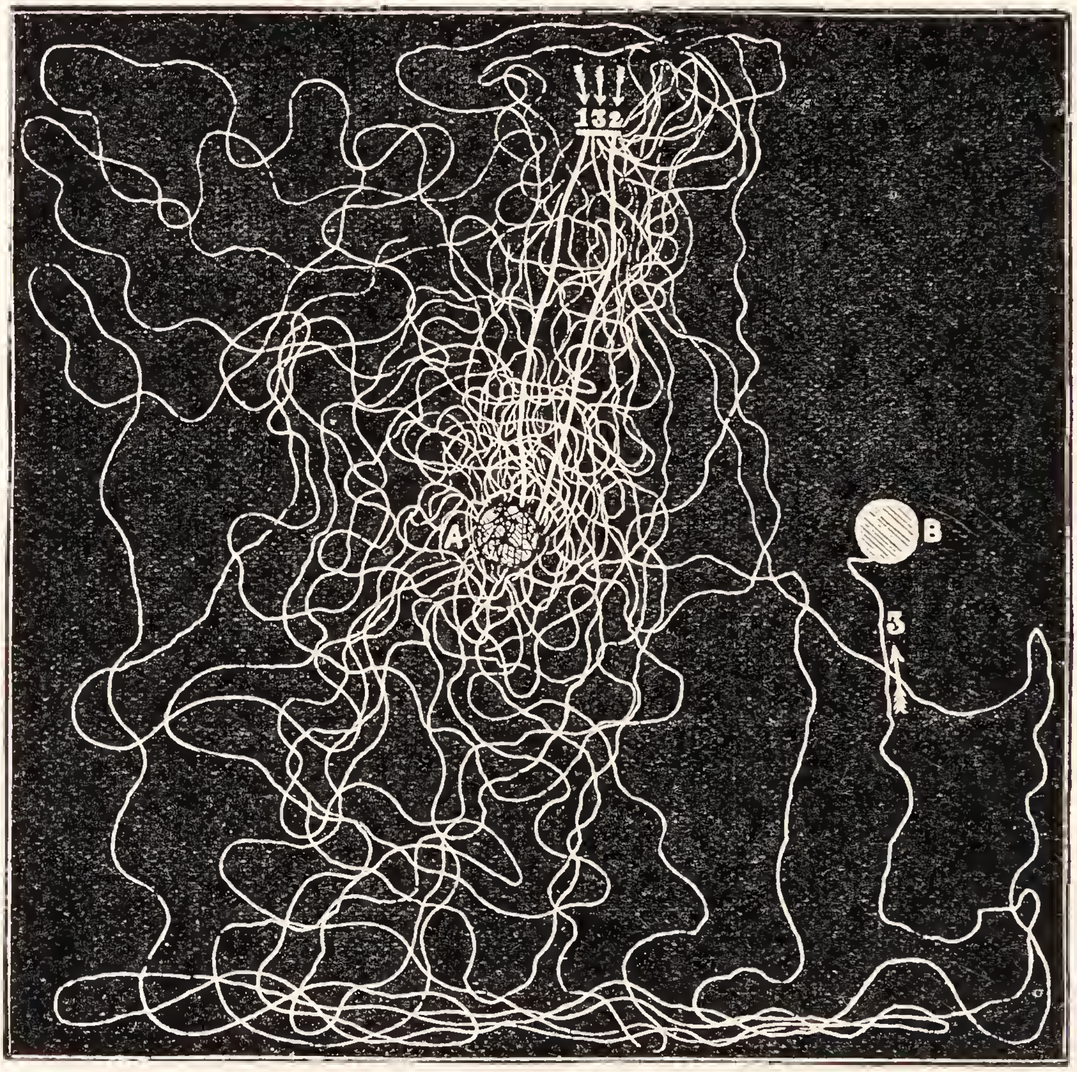


Diagram of complex path traversed in experiment 4.

A, first position of pencil. B, second position of pencil. 1, 2, straight lines of two tracks of the observed ants. 3, winding narrow white line, showing course pursued by the same ant before arriving at B, when the position of the pencil was unchanged.

anticipated, seems to follow from the fact that after the pencil and tray of larvæ had been removed but a short distance to the right or left, the ants on their journey to the shifted object travelled very often backwards and forwards and around the spot where the coveted object first stood. Then they would retrace their steps towards the nest, wander hither and thither from side to side between the nest and the point A, and only after very repeated efforts around the original site of the larvæ reach, as it were accidentally, the object desired at B.

Fig. 16.

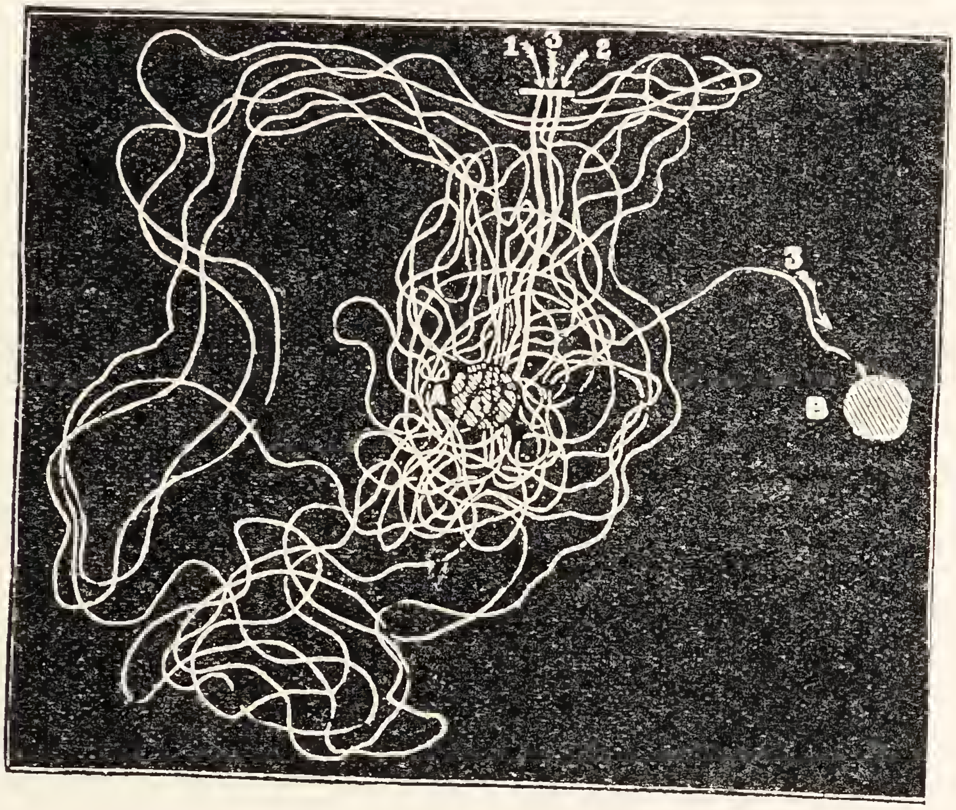


Diagram representing three tracks of an ant in another experiment.

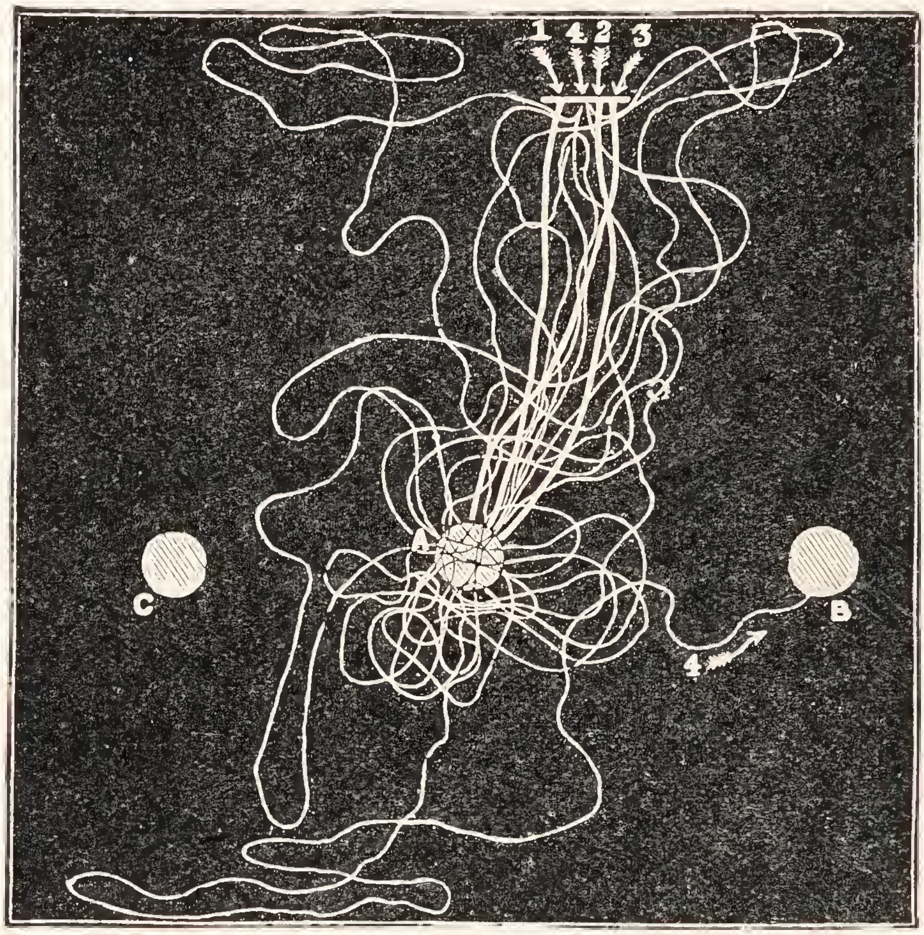
A, the first position of pencil and the food, towards which and from the base-line of nest 1 and 2 lead by nearly direct broadish white lines to A. When the latter was removed to B the ant, in its effort to reach this, pursued the narrow white winding line ending in 3 →.

Another evidence of this consists in the fact that if when ants (*L. niger*) were carrying off larvæ placed in a cup on a piece of board, I turned the board round so that the side which had been turned towards the nest was away from it, and *vice versâ*, the ants always returned over the same track on the board, and, in consequence directly away from home.

If I moved the board to the other side of my artificial nest, the result was the same. Evidently they followed the road, not the direction.

In order further to test how far ants are guided by sight and how much by scent, I tried the following experiment with *Lasius niger*. Some food was put out

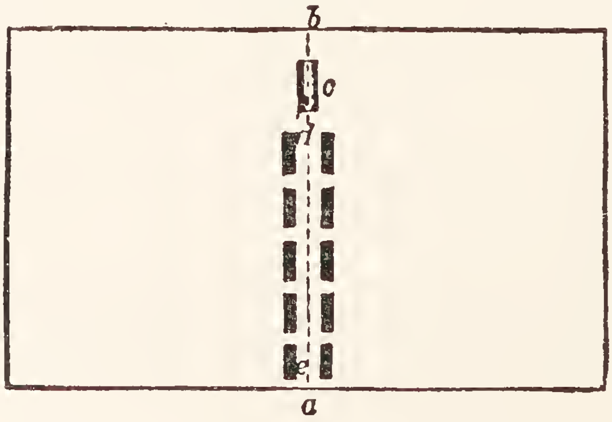
Fig. 17.



Another tracing showing a similar experiment. 1, 2, 3, the direct broad lines towards A; and 4, the complicated track made when reservoir of larvæ was removed to B.

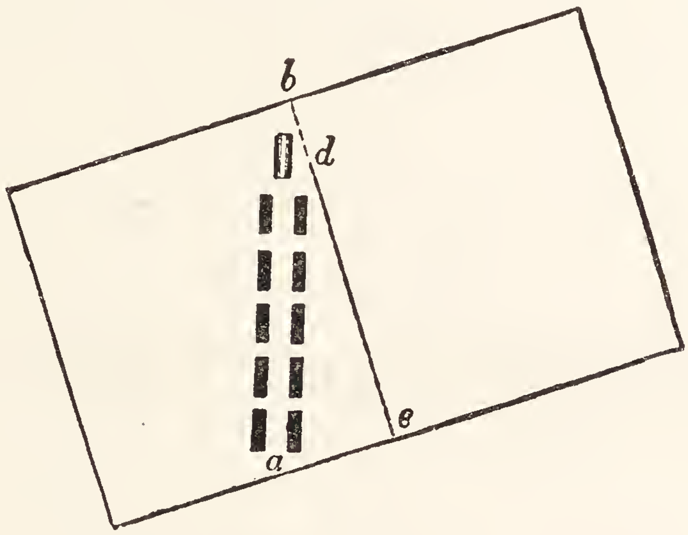
at the point *a* on a board measuring 20 inches by 12 (Fig. 18), and so arranged that the ants in going straight

Fig. 18.



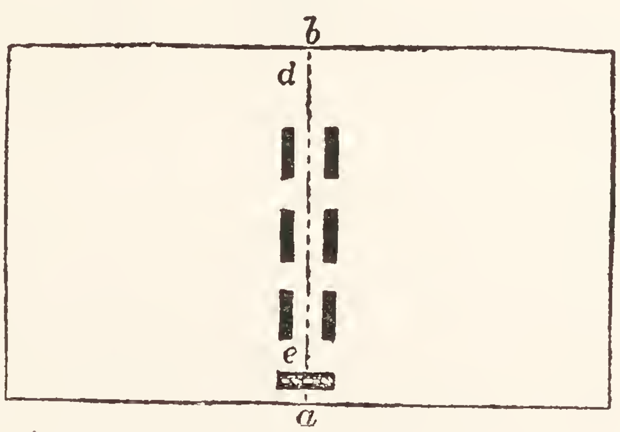
to it from the nest would reach the board at the point *b*, and after passing under a paper tunnel, *c*, would proceed between five pairs of wooden bricks, each 3 inches in length and $1\frac{3}{4}$ in height. When they got to know their way, they went quite straight along the line *d e* to *a*. The

Fig. 19.



board was then twisted as shown in Fig. 19. The bricks and tunnel being also rearranged so that they were exactly in the same direction as before, but the board having been moved, the line *d e* was now outside them. This change, however, did not at all discompose the

Fig. 20.



ants; but instead of going, as before, through the tunnel and between the rows of bricks to *a*, they walked exactly along the old path to *e*.

I then arranged matters as before, but without the tunnel and with only three pairs of bricks (Fig. 20). When an ant had got quite used to the path *d* to *e*, I altered the position of the bricks and food, as shown in Fig. 21, making a difference of 8 inches in the position of the latter. The ant came as before, walked up to the first brick, touched it with her antennæ, but then followed her old line to *a*. From there she veered towards the food, and very soon found it. When she was gone, I altered it again, as shown in Fig. 22; she returned after the usual interval

Fig. 21.

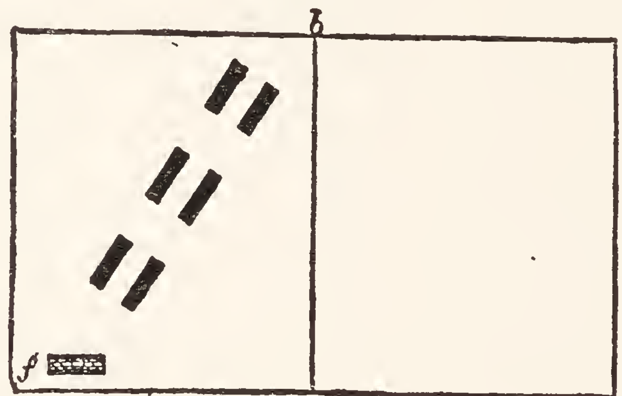
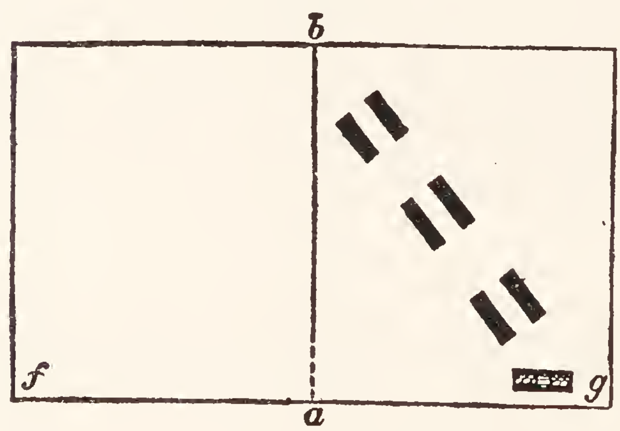


Fig. 22.



and went again straight to *a*; then, after some wanderings, to *f*, and at length, but only after a lapse of 25 minutes, found the food at *g*. These experiments were repeated more than once, and always with similar results. I then varied matters by removing the bricks, which, however, did not seem to make any difference to the ants.

I then accustomed some ants (*Lasius niger*) to go to and fro over a wooden bridge, *b*, *c* (Fig. 23), to some food.

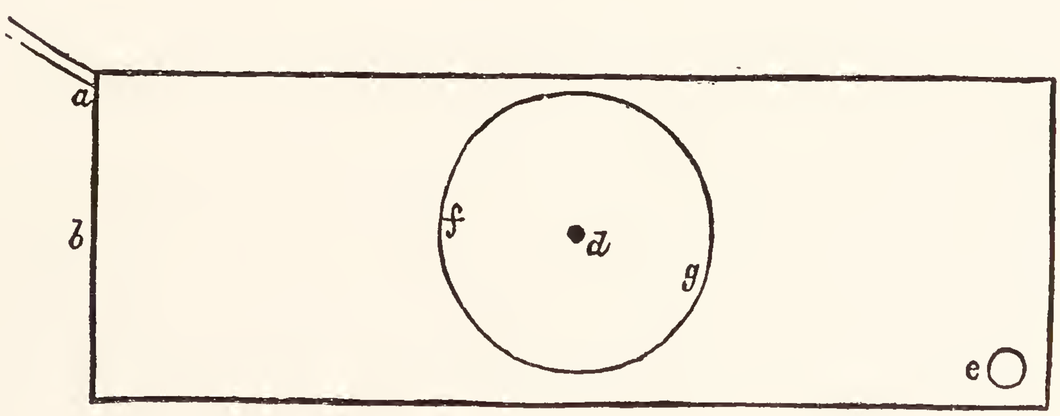
When they had got quite accustomed to the way, I watched when an ant was on the bridge and then turned it round, so that the end *b* was at *c*, and *c* at *b*. In most cases the ant immediately turned round also; but even if she went on to *b* or *c*, as the case may be, as soon as she came to the end of the bridge she turned round.

Fig. 23

I then modified the arrangement, placing between the nest and the food three similar pieces of wood. Then when the ant was on the middle piece, I transposed the other two. To my surprise this did not at all disconcert them.

I then tried the arrangement shown in Fig. 24.

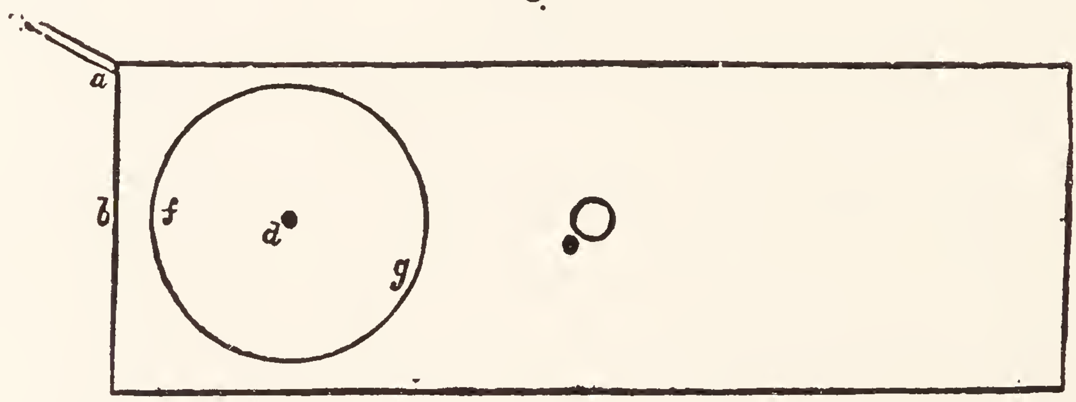
Fig. 24.



a is a paper bridge leading to the nest; *b* is a board about 22 inches long by 13 broad, on which is a disk of white paper fastened at the centre by a pin *d*; *e* is some food. When the ants had come to know their way so that they passed straight over the paper disk on their way from *a* to *e*, I moved the disk round with an ant on it, so that *f* came to *g* and *g* to *f*. As before, the ants turned round with the paper.

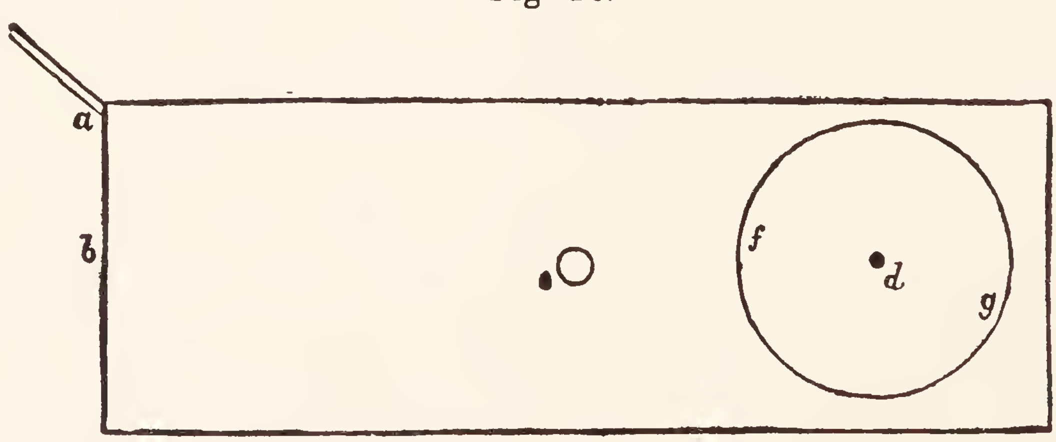
As it might be possible that the ants turned round on account of the changed relative position of external objects, I next substituted a circular box 12 inches in diameter, open at the top, and 7 inches high (in fact, a hat-box) for the flat paper, cutting two holes at *f* and *g*, so that the ants passing from the nest to the food went through the box entering at *f* and coming out at *g*. The box was fixed at *d*, so that it might turn easily. I then,

Fig. 25.



when they had got to know their way, turned the box round as soon as an ant had entered it, but in every case the ant turned round too, thus retaining her direction. I then varied the experiment as shown in Figs. 25 and 26.

Fig. 26.

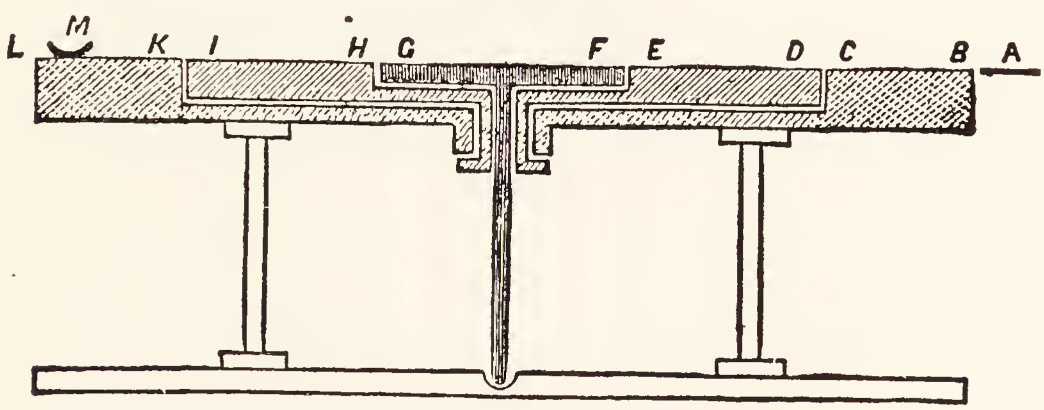


I replaced the white disk of paper, but put the food *e* at the middle of the board. When the ant had got used to this arrangement I waited till one was on the disk (Fig. 25) and then gently drew it to the other side of *e*, as shown in Fig. 26. In this case, however, the ant did not turn round, but went on to *g*, when she seemed a good deal surprised at finding where she was.

In continuation of the preceding experiments I constructed a circular table 18 inches in diameter. It consisted, as shown in Figs. 27 and 28, of three concentric pieces—a central F G, an intermediate D E, H I, and an outer piece B C, K L, each of these three pieces being capable of separate rotation. This arrangement was kindly devised for me by Mr Francis Galton.

I then connected the table with a nest of *Lasius niger* by a paper bridge A, and also made a paper path across the table, as shown in Fig. 28, divided into five pieces corresponding to the divisions of the table. This I did because I found that the ants wandered less if they were provided with a paper road than if they walked

Fig. 27.

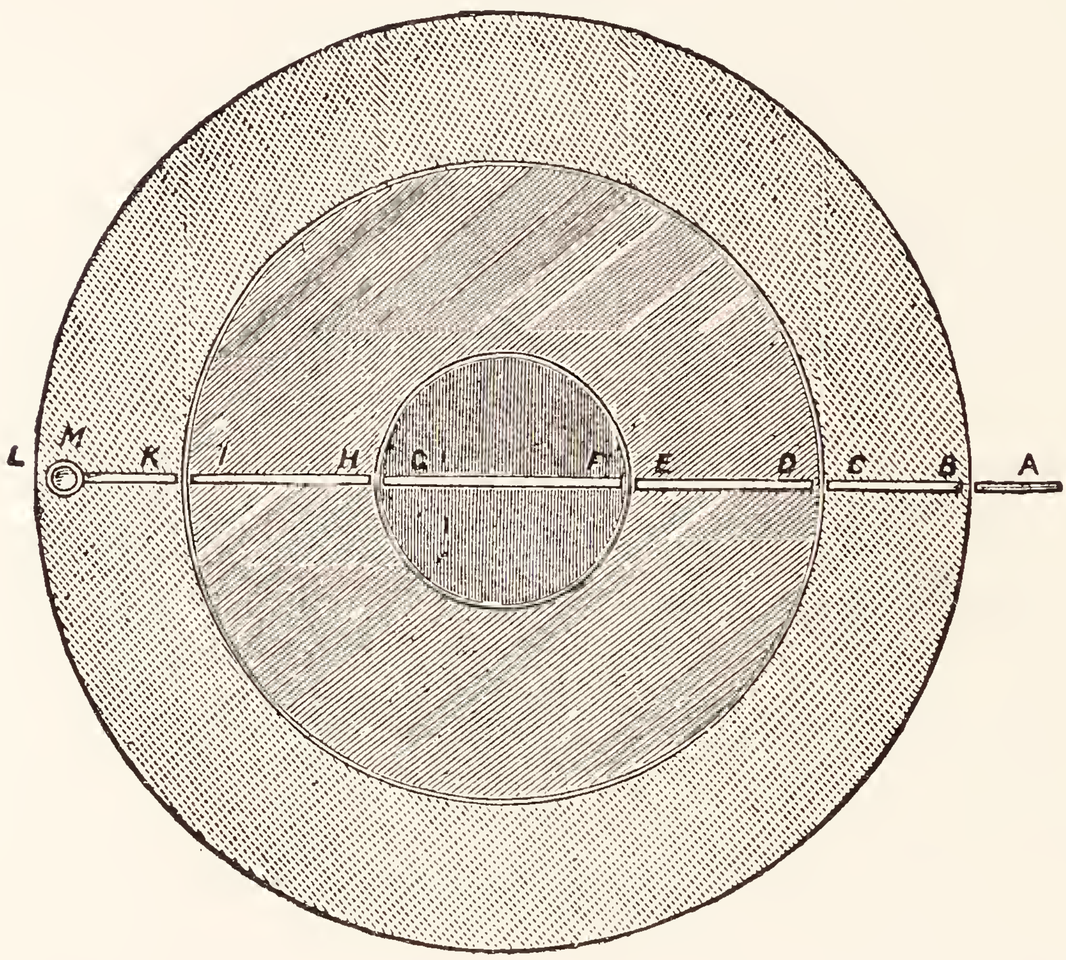


actually on the wood itself. I then placed a cup containing larvæ on the table at B, and put an ant on the larvæ. She at once picked one up, and, with some little guidance from me, carried it off to the nest, returning at once for another, bringing some friends with her to help. When she knew her way, I gradually moved the cup across the table along the paper path to M, placing it on a column five inches high. After a while the ants came to know the way quite well, and passed straight along the path from the nest to the larvæ at M. Having thus established a service of ants, I tried the following experiments :—

1. I removed the piece of paper G F. This disturbed them ; but they very soon re-established the chain.

2. I turned round the central piece of the table G F, so that the paper G F was reversed, G being where F had been, and *vice versâ*. This did not seem to disconcert the ants at all. They went straight over the paper as before, without a moment's hesitation.

Fig. 28.



3. When some ants were between I and D, I rotated the outer circle of the table half way round, which of course carried the cup containing the larvæ from L to B. The ants took no notice of this, but went straight to L.

4. When some ants were between I and D, I rotated the table several times, bringing it finally to its original position. This disturbed them a good deal, but eventually they all continued their course to L.

5. When some ants were between I and D, I half rotated the two centre parts of the table, the result of which, of course, was that the ant was moving towards, instead of away from, the nest. In every case the ants turned round too, so as duly to reach L. So also those

which were on their way back from the larvæ to the nest turned in the same manner.

6. When the ants were between I and D, I half rotated the whole table. Again the ants turned round too, though, of course, in this case when they reached the place where L had been, the cup with the larvæ was behind them at B.

The two later experiments, though quite in accordance with those previously made, puzzled me a good deal. Experiment 3, as well as some of those recorded previously, seemed to show that the ants were little guided in such cases by the position of surrounding objects. However, I was anxious to test this.

7. Accordingly I took a round box and placed it upside down on the table, having cut two niches, one at each side, where it lay on the paper path, so as to afford a passage for the ants, as in the experiments recorded in my previous paper; but on this occasion I left the lid on, cutting, however, a hole through which I could watch the result. In this case, therefore, the surrounding objects, i.e. the walls of the box, turned round with the table. Then, as before, when the ants were between I and D, I turned the table half round. The results were as follows :—

	Ants which turned.	Ants which did not turn.
Experiment 1 . .	1	2
,, 2 . .	1	1
,, 3 . .	1	1
,, 4 . .	4	2
,, 5 . .	0	1
,, 6 . .	0	1
,, 7 . .	0	3
,, 8 . .	1	1
,, 9 . .	0	1
,, 10 . .	2	2
,, 11 . .	1	1
,, 12 . .	0	3
	11	19

In this case, then, only 11 ants turned; and as 4 of them were together, it is possible that 3 simply followed the first. Moreover, the ants which turned did so with much more hesitation and less immediately.

8. For comparison, I then again tried the same experiment, but without the box. The results were as follows :—

Observation.	Ants which turned.	Ants which did not turn.
1	3	0
2	3	0
3	3	1 ?
4	3	0
5	4	0
6	4	0
	20	1

Under these circumstances, therefore, all the ants but one certainly turned, and her movements were undecided.

From these last two experiments it is obvious that the presence of the box greatly affected the result, and yet the previous results made it difficult to suppose that the ants noticed any objects so distant as the walls of the rooms, or even as I was myself. The result surprised me considerably; but I think the explanation is given by the following experiments.

I again put some larvæ in a cup, which I placed in the centre of the table; and I let out an ant which I had imprisoned after the previous experiments, placing her in the cup; she carried off a larva to the nest and soon returned. When she was again in the cup I half rotated the table: when she came out she seemed a little surprised; but after walking once round the cup, started off along the paper bridge straight home. When she returned to the cup I again half rotated the table. This time she went back quite straight. When she had come again, I once more half rotated the table; she returned quite straight. Again the same happened. A second ant then came I half rotated the table as before. She went wrong for about an inch and a half, but then turned round and went straight home.

I was working by the light of two candles which were on the side of the table towards the nest. The next time the two ants came I half rotated the table as before, and moved the candles to the far side. This time the ants were deceived, and followed the paper bridge to the end of the table furthest from the nest. This I repeated a second time, with the same result. I then turned the table as before without altering the lights and the ants (four of them) went back all right. I then again turned the table, altering the lights, and the ant went wrong.

I then altered the lights without rotating the table: the first ant went wrong; the second right; the third wrong; the fourth wrong; the fifth hesitated some seconds, and then went wrong; the sixth right; the seventh went all but to the edge the wrong way, but, after various wanderings, at last went right. When, therefore, the direction of the light was changed but everything else left as before, out of seven ants, five were deceived and went in the wrong direction.

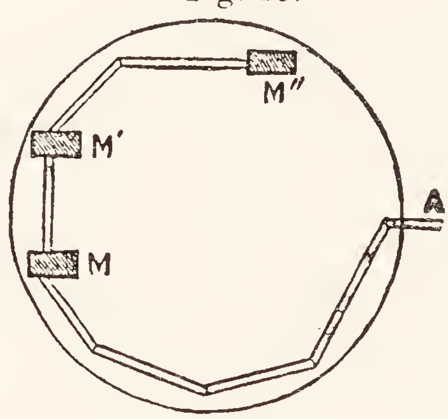
After an interval of a week, on 25th March, I arranged the nest and the rotating table as before, and let out three ants which I had imprisoned on the 19th, and which knew their way. I put them on the larvæ at M as before. The paper pathway had been left untouched. The ants examined the larvæ and then went straight home along the paper path; but, to my surprise, only one of them carried off a larva. Nevertheless they had evidently taken the news to the nest, for the ants at once began coming to the cup in considerable numbers and carrying off the larvæ. I do not altogether understand this proceeding, and unluckily had not marked the first three ants; so that I cannot tell whether they brought or sent their friends. It seems possible that they felt unequal to the exertion of carrying a burthen to the nest until they had had some food.

When the ants were fairly at work I turned the table 90 degrees. In this case eight ants which were on their way to the larvæ continued their march along the paper, while two turned back; but none left the paper and went across the table straight for the larvæ.

I then stopped the experiment for a while, so that the excitement might subside; as when the ants become too numerous it is not so easy to watch them.

When all was quiet I put the cup with the larvæ on the middle of the table, and covered the greater part of the table with the box as before. In a short time some ants again came to the larvæ, and then, just as

Fig. 29.



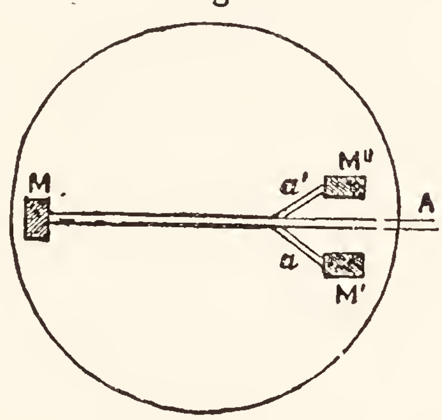
they were leaving the cup on their way home, I turned the table, as before, half round.

Under these circumstances, however, instead of turning as in the previous experiment, ten ants, one after another, continued their course, thus coming out of the box at the end furthest from the nest. When ten ants successively had, under these circumstances gone wrong, to make the experiment complete, I tried it again, everything being the same, except that there was no box. Under these circumstances five ants, one after the other, turned directly the table was rotated.

From these experiments, therefore, it seems clear that in determining their course the ants are greatly influenced by the direction of the light.

27th March.—I let out two ants imprisoned on the 25th, and placed them on the larvæ, which I put on a column 7 inches high, covered with blue paper, and communicating with the nest by the paper path (A, Fig. 29) arranged as usual, but supported on pins. At first I arranged it as shown below, placing the larvæ at M, on a table 18 inches in diameter, so that the ants, on arriving at the larvæ, made nearly a semi-circle round the edge of the table. I then gradually moved the larvæ to M′ and afterwards to M″. The ants, however, obviously knew that they were going unnecessarily round. They ran along the paper bridge in a very undecided manner, continually turning round and often coming down the pins; while in returning to the nest they persistently

Fig. 30.



came down the side of the pillar nearest to the nest, though I repeatedly attempted to guide them the other way. Even when placed on the paper bridge between M and M′, they were very dissatisfied. In fact, it was obvious that they knew they were being sent a long way round, and were attempting to make a shorter cut.

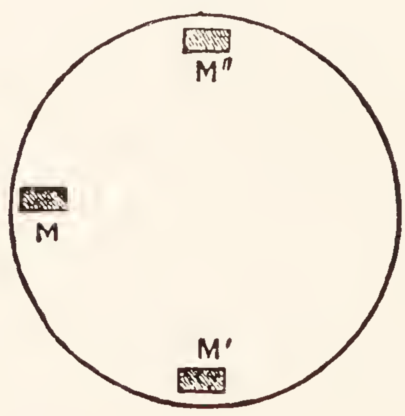
I then again placed the larvæ on the column at M, and when the ants were once more going to and fro regularly along the paper path, I altered the position of the column and larvæ to M′, placing the edge of the pillar, which the ants had been accustomed to ascend, towards the paper bridge, connecting it with the original bridge by a side-bridge *a*, M being an inch from the original bridge. Under these circumstances three ants ran on to

M; then two found their way over the bridge *a* to M′. Of the next ten ants, five went to M and five over *a* to M′. The next ten all went over the paper bridge *a* to M′.

I then put the pillar and the larvæ on the other side of the original paper path at M″, connected with the mainpath by a short bridge *a′*, taking for *a′* a new piece of paper, so that scent would be no guide. I left the little bridge *a* in its place. The ants went as follows:—

To M″	1	To M′	0	To M	0
,,	1	,,	0	,,	1
,,	1	,,	0	,,	1
,,	1	,,	0	,,	1
,,	1	,,	1	,,	1
,,	0	,,	0	,,	1
,,	1	,,	0	,,	0
,,	1	,,	0	,,	0
,,	1	,,	0	,,	0
,,	1	,,	0	,,	0
,,	1	,,	1	,,	0
,,	1	,,	1	,,	0
,,	1	,,	0	,,	0
	12		3		5

Fig. 31.



It seems clear, therefore, that though the ants did not trust so much to their eyes as a man would have done under similar circumstances, yet that they were to some extent guided by sight.

I then removed all the paper pathways and put the pillar to M. Of the first two ants which came to the table, the first found the pillar in five minutes, the second, after wandering about for a quarter of an hour, gave the search up in despair, and went home. I then moved the pillar to M′, and watched the next ant that came on to the table; she found it in a minute or two. I then moved it to M″. Two ants came together. One found the pillar in 7 minutes; the other took no less than 25, although, as already mentioned, the table was only 18 inches in diameter. Obviously, therefore, though it seems clear that they are helped by sight, still these last observations support those previously recorded, and show that in finding their way they do not derive by any means so much assistance from their eyes as we should do under corresponding circumstances.[54]

CHAPTER X

BEES

I ORIGINALLY intended to make my experiment principally with bees, but soon found that ants were on the whole more suitable for my purpose.

In the first place, ants are much less excitable, they are less liable to accidents, and from the absence of wings are more easy to keep under continuous observation.

Still, I have made a certain number of observations with bees, some of which may be worth here recording.

As already mentioned, the current statements with reference to the language of social insects depend much on the fact that when one of them, either by accident or in the course of its rambles, has discovered a stock of food, in a very short time many others arrive to profit by the discovery. This, however, does not necessarily imply any power of describing localities. If the bees or ants merely follow their more fortunate comrade, the matter is comparatively simple ; if, on the contrary, others are sent, the case becomes very different.

In order to test this I proposed to keep honey in a given place for some time, in order to satisfy myself that it would not readily be found by the bees ; and then, after bringing a bee to the honey, to watch whether it brought others, or sent them—the latter of course implying a much higher order of intelligence and power of communication.

I therefore placed some honey in a glass, close to an open window in my sitting-room, and watched it for sixty hours of sunshine, during which no bees came to it.

I then, at 10 a.m. on a beautiful morning in June, went to my hives, and took a bee which was just starting out, brought it in my hand up to my room (a distance of somewhat less than 200 yards), and gave it some honey, which it sucked with evident enjoyment. After a few minutes it flew quietly away, but did not return ; nor did any other bee make its appearance.

The following morning I repeated the same experiment. At 7.15 I brought up a bee, which sipped the honey with readiness, and after doing so for about four minutes flew away with no appearance of alarm or annoyance. It did not, however, return ; nor did any other bee come to my honey.

On several other occasions I repeated the same experiments with a like result. Altogether I tried it more than twenty times. Indeed, I rarely found bees to return to honey if brought any considerable distance at once. By taking them, however, some twenty yards each time they came to the honey, I at length trained them to come to my room. On the whole, however, I found it more convenient to procure one of Marriott's observatory hives, both on account of its construction, and also because I could have it in my room, and thus keep the bees more immediately under my own eye. My room is square, with three windows, two on the south-west side, where the hive was placed, and one on the south-east. Besides the ordinary entrance from the outside, the hive had a small postern door opening into the room ; this door was provided with an alighting board, and close by a plug : as a general rule the bees did not notice it much unless the passage was very full of them.

I then placed some honey on a table close to the hive, and from time to time fed certain bees on it. Those which had been fed soon got accustomed to come for the honey ; but partly on account of my frequent absence from home, and partly from their difficulty in finding their way about, and their tendency to lose themselves, I could never keep any marked bee under observation for more than a few days.

Out of a number of similar observations I will here mention a few as throwing some light on the power of communicating facts possessed by bees; they will also illustrate the daily occupations of a working bee.

Experiment 1.—Thus, on 24th August, 1874, I opened the postern door leading into my room at 6.45 a.m., and watched till 1 p.m. three bees, which had been trained to come to honey at a particular spot. They did not, however, know their way very well, and consequently lost a good deal of time. One made 23 journeys backwards and forwards between the hive and the honey, the second 13, and the third only 7.

The following day I watched the first of these bees from 7.23 to 12.54, during which time she made 19 journeys. Scarcely any other bees came, but I did not record the exact number.

Experiment 2.—I watched another bee from 6.55 a.m. till 7.15 p.m., during which time she made 59 visits to the honey, and only one other bee came to it.

Experiment 3.—Another from 7 a.m. till 3 p.m.; she made 40 journeys, and only two other bees came. She returned the two following mornings, and was watched for three hours each day, during which time no other bee came.

Experiment 4.—Another morning I watched a different bee from 9.19 a.m. to 2 p.m.; she made 21 journeys, and no other bee came.

Then, thinking perhaps this result might be due to the quantity of honey being too small, I used a wide-mouthed jar, containing more than one pound of honey.

Experiment 5.—I watched two bees from 1.44 till 4.30, during which time they made 24 journeys, but only one other bee came.

Experiment 6.—Besides the honey in the jar I spread some out over two plates, so as to increase the surface. I watched a bee from 12.15 till 6.15 p.m. She made 28 journeys, but did not bring a single friend with her.

Experiment 7.—On 19th July I put a bee to a honeycomb which contained twelve and a half pounds of honey at 12.30, and which was placed in a corner of my room as far as possible from the window. That afternoon she made 22 visits to it, and no other bee came. The following morning she returned at 6.5 a.m., and I watched her till 2. She made 22 journeys, but did not bring a single friend with her.

Experiment 8.—Another bee was also brought to the same honeycomb, watched from 2.30 till 7.14. She made 14 journeys, but did not bring a single friend.

I might give other similar cases, but these are, I think, sufficient to show that bees do not bring their friends to share any treasure they have discovered, so invariably as might be assumed from the statements of previous observers.[55] Possibly the result is partly due to the fact that my room is on the first floor, so that the bees coming to it flew at a higher level than that generally used by their companions, and hence were less likely to be followed.

Indeed, I have been a good deal surprised at the difficulty which bees experience in finding their way.

For instance, I put a bee into a bell-glass 18 inches long, and with a mouth 6½ inches wide, turning the closed end to the window; she buzzed about for an hour, when, as there seemed no chance of her getting out, I put her back into the hive. Two flies, on the contrary, which I put in with her, got out at once. At 11.30 I put another bee and a fly into the same glass; the latter flew out at once. For half an hour the bee tried to get out at the closed end; I then turned the glass with its open end to the light, when she flew out at once. To make sure, I repeated the experiment once more with the same result.

Some bees, however, have seemed to me more intelligent in this respect than others. A bee which I have fed several times, and which had flown about in the room, found its way out of the glass in a quarter of an hour, and when put in a second time came out at once. Another bee, when I closed the postern door which opened from my hive directly into my room, used to come round to the honey through an open window.

One day (14th April, 1872), when a number of them were very busy on some berberries, I put a saucer with some honey between two bunches of flowers; these flowers were repeatedly visited, and were so close that there was hardly room for the saucer between them, yet from 9.30 to 3.30 not a single bee took any notice of the honey. At 3.30 I put some honey on one of the bunches of flowers, and it was eagerly sucked by the bees; two kept continually returning till past five in the evening.

One day when I came home in the afternoon I found that at least a hundred bees had got into my room through the postern and were on the window, yet not one was attracted by an open jar of honey which stood in a shady corner about 3 ft. 6 in. from the window.

Another day (29th April, 1872) I placed a saucer of honey close to some forget-me-nots, on which bees were numerous and busy; yet from 10 a.m. till 6 only one bee went to the honey.

I put some honey in a hollow in the garden wall opposite my hives at 10.30 (this wall is about five feet high and four feet from the hives), yet the bees did not find it during the whole day.

On 30th March, 1873, a fine sunshiny day, when the bees were very active, I placed a glass containing honey at 9 in the morning on the wall in front of the hives; but not a single bee went to the honey the whole day. On 20th April I tried the same experiment with the same result.

19th September.—At 9.30 I placed some honey in a glass about four feet from and just in front of the hive, but during the whole day not a bee observed it.

As it then occurred to me that it might be suggested that there was something about this honey which rendered it unattractive to the bees, on the following day I first placed it again on the top of the wall for three hours, during which not a single bee came, and then moved it close to the alighting board of the hive. It remained unnoticed for a quarter of an hour, when two bees observed it, and others soon followed in considerable numbers.

It is generally stated not only that the bees in a hive all know one another, but also that they immediately recognize and attack any intruder from another hive. It is possible that the bees of particular hives have a particular smell. Thus Langstroth, in his interesting *Treatise on the Honey-Bee,* says "Members of different colonies appear to recognize their hive companions by the sense of smell"; and I believe that if colonies are sprinkled with scented syrup they may generally be safely mixed. Moreover, a bee returning to its own hive with a load of treasure is a very different creature from a hungry marauder; and it is said that a bee, if laden with honey, is allowed to enter any hive with impunity. Dr Langstroth continues: "There is an air of roguery about a thieving bee which, to the expert, is as characteristic as are the motions of a pickpocket to a skilful policeman. Its sneaking look and nervous, guilty agitation, once seen, can never be mistaken." It is at any rate natural that a bee which enters a wrong hive by accident should be much surprised and alarmed, and would thus probably betray herself.

So far as my own observations go, though bees habitually know and return to their own hive, still, if placed on the alighting-board of another, they often enter it without molestation. Thus:—

On 4th May I put a strange bee into a hive at 2 o'clock. She remained in till 2.20, when she came out, but entered again directly. I was away most of the afternoon, but returned at 5.30; at 6 she came out of the hive but soon returned; and after that I saw no more of her.

12th May.—A beautiful day, and the bees very active. I placed twelve marked bees on the alighting-board of a neighbouring hive. They all went in ; but before evening ten had returned home.

13th May.—Again put twelve marked bees on the alighting-board of another nest ; eleven went in. The following day I found that seven had returned home ; the other five I could not see.

17th May.—Took a bee, and, after feeding her and marking her white, put her to a hive next but one to her own at 4.18. She went in.

4.22. Came out and went in again.
4.29. Came out. I fed her and sent her back.
4.35. Came out. Took a little flight and came back.
4.45. Went in, but returned. 4.52. Went in.
4.53. Came out. 4.56. ,,
4.57. ,, 4.58. ,,
5. 1. Came out, took another little flight, and returned. I fed her again. 5.25. Went in again.
5.28. Came out again. 5.29. ,,
5.31. ,, 5.33. ,,
5.36. ,, 5.40. ,,
5.46. Shut her and the others in with a piece of notepaper.
6.36. One of the bees forced her way through. I opened the door, and several, including the white one, came out directly. Till 6.50 this bee kept on going in and out every minute or two ; hardly any bees were flying, only a few standing at the doors of most of the hives. At 7.20 she was still at the hive door.

20th May.—Between 6 and 7 p.m. I marked a bee and transferred her to another hive.

21st May.—Watched from 7.30 to 8.9 in the morning without seeing her. At half-past six in the evening went down again, directly saw and fed her. She was then in her new hive ; but a few minutes after I observed her on the lighting-stage of her old hive ; so I again fed her, and when she left my hand she returned to the new hive.

22nd May.—8 o'clock. She was back in her old hive.

23rd May.—About 12.30 she was again in the new hive.

Though bees which have stung and lost their sting always perish, they do not die immediately; and in the meantime they show little sign of suffering from the terrible injury. On 25th August a bee which had come several times to my honey was startled, flew to one of the windows, and had evidently lost her way. While I was putting her back she stung me, and lost her sting in doing so. I put her in through the postern, and for twenty minutes she remained on the landing-stage; she then went into the hive, and after an hour returned to the honey and fed quietly, notwithstanding the terrible injury she had received. After this, however, I did not see her any more.

Like many other insects, bees are much affected by light. One evening, having to go down to the cellar, I lit a small covered lamp. A bee which was out came to it, and, flying round and round like a moth, followed me the whole of the way there.

I often found that if bees which were brought to honey did not return at once, still they would do so a day or two afterwards. For instance, on 11th July, 1874, a hot, thundery day, and when the bees were much out of humour, I brought twelve bees to some honey: only one came back, and that one only once; but on the following day several of them returned.

My bees sometimes ceased work at times when I could not account for their doing so. 19th October was a beautiful, sunshiny, warm day. All the morning the bees were fully active. At 11.25 I brought one to the honeycomb, and she returned at the usual intervals for a couple of hours; but after that she came no more, nor were there any other bees at work. Yet the weather was lovely, and the hive is so placed as to catch the afternoon sun.

I have made a few observations to ascertain, if possible, whether the bees generally go to the same part of the hive. Thus:—

5th October.—I took a bee out of the hive, fed her, and marked her. She went back to the same part.

9th October.—At 7.15 I took out two bees, fed and marked them. They returned; but I could not see them in the same part of the hive. One, however, I found not far off.

At 9.30 brought out four bees, fed and marked them. One returned to the same part of the hive. I lost sight of the others.

Since their extreme eagerness for honey may be attributed rather to their anxiety for the commonweal than to their desire for personal gratification, it cannot fairly be imputed as greediness; still the following scene, described by Dr. Langstroth, and one which most of us have witnessed, is incompatible surely with much intelligence. "No one can understand the extent of their infatuation until he has seen a confectioner's shop assailed by myriads of hungry bees. I have seen thousands strained out from the syrup in which they had perished; thousands more alighting even upon the boiling sweets; the floor covered and windows darkened with bees, some crawling, others flying, and others still so completely besmeared as to be able neither to crawl nor fly—not one in ten able to carry home its ill-gotten spoils, and yet the air filled with new hosts of thoughtless comers." *

If, however, bees are to be credited with any moral feelings at all, I fear the experience of all bee-keepers shows that they have no conscientious scruples about robbing their weaker brethren. "If the bees of a strong stock," says Langstroth, "once get a taste of forbidden sweets, they will seldom stop until they have tested the strength of every hive." And again, "Some bee-keepers question whether a bee that once learns to steal ever returns to honest courses." Siebold has mentioned similar facts in the case of certain wasps (*Polistes*).

Far, indeed, from having been able to discover any

* *Hive- ana Honey-Bee*, Langstroth, p. 277.

evidence of affection among them, they appear to be thoroughly callous and utterly indifferent to one another. As already mentioned, it was necessary for me occasionally to kill a bee; but I never found that the others took the slightest notice. Thus on 11th October I crushed a bee close to one which was feeding—in fact, so close that their wings touched; yet the survivor took no notice whatever of the death of her sister, but went on feeding with every appearance of composure and enjoyment, just as if nothing had happened. When the pressure was removed, she remained by the side of the corpse without the slightest appearance of apprehension, sorrow, or recognition. She evidently did not feel the slightest emotion at her sister's death, nor did she show any alarm lest the same fate should befall her also. In a second case exactly the same occurred. Again, I have several times, while a bee has been feeding, held a second bee by the leg close to her; the prisoner, of course, struggled to escape, and buzzed as loudly as she could; yet the bee which was feeding took no notice whatever. So far, therefore, from being at all affectionate, I doubt whether bees are in the least fond of one another.

Their devotion to their queen is generally quoted as an admirable trait; yet it is of the most limited character. For instance, I was anxious to change one of my black queens for Ligurian; and accordingly on 26th October Mr Hunter was good enough to bring me a Ligurian queen. We removed the old queen, and we placed her with some workers in a box containing some comb. I was obliged to leave home on the following day; but when I returned on the 30th I found that all the bees had deserted the poor queen, who seemed weak, helpless, and miserable. On the 31st the bees were coming to some honey at one of my windows, and I placed this poor queen close to them. In alighting, several of them even touched her; yet not one of her subjects took the slightest notice of her. The same queen, when afterwards placed in the hive, immediately attracted a number of bees.

As regards the affection of bees for one another, it is no doubt true that when they have got any honey on them, they are always licked clean by the rest ; but I am satisfied that this is for the sake of the honey rather than of the bee. On 27th September, for instance, I tried with two bees ; one had been drowned, the other was smeared with honey. The latter was soon licked clean ; of the former they took no notice whatever. I have, moreover, repeatedly placed dead bees by honey on which live ones were feeding, but the latter never took the slightest notice of the corpses.

Dead bees are indeed usually carried out of the hive ; but if one is placed on the alighting-stage, the others seem to take no notice of it, though it is in general soon pushed off accidentally by their movements. I have even seen the bees sucking the juices of a dead pupa.

As regards the senses of bees, it seems clear that they possess a keen power of smell.

On 5th October I put a few drops of eau-de-Cologne in the entrance of one of my hives, and immediately a number of bees (about fifteen) came out to see what was the matter. Rose-water also had the same effect ; and, as will be mentioned presently, in this manner I called the bees out several times ; but after a few days they took hardly any notice of the scent.

These observations were made partly with the view of ascertaining whether the same bees act as sentinels. With this object, on 5th October I called out the bees by placing some eau-de-Cologne in the entrance, and marked the first three bees that came out. At 5 p.m. I called them out again ; about twenty came, including the three marked ones. I marked three more.

6th October.—Called them out again. Out of the first twelve, five were marked ones. I marked three more.

7th October.—Called them out at 7.30 a.m. as before. Out of the first nine, seven were marked ones.

At 5.30 p.m. called them out again. Out of six, five were marked ones.

8th October.—Called them out at 7.15. Six came out, all marked ones.

9th October.—Called them out at 6.40. Out of the first ten, eight were marked ones.

Called them out at 11.30 a.m. Out of six, three were marked. I marked the other three.

Called them out at 1.30 p.m. Out of ten, six were marked.

Called them out at 4.30. Out of ten, seven were marked.

10th October.—Called them out at 6.5 a.m. Out of six, five were marked.

Shortly afterwards, I did the same again, when out of eleven, seven were marked ones.

5.30 p.m. Called them out again. Out of seven, five were marked.

11th October.—6.30 a.m. Called them out again. Out of nine, seven were marked.

5 p.m. Called them out again. Out of seven, five were marked.

After this day, they took hardly any notice of the scents.

Thus in these nine experiments, out of the ninety-seven bees which came out first, no less than seventy-one were marked ones, though out of the whole number of bees in the hive there were only twelve marked for this purpose, and, indeed, even fewer in the earlier experiments. I ought, perhaps, to add that I generally fed the bees when I called them out.

The Sense of Hearing

The result of my experiments on the hearing of bees has surprised me very much. It is generally considered that to a certain extent the emotions of bees are expressed by the sounds they make,* which seems to imply that they possess the power of hearing.

* See, for instance, Landois, *Zeits. f. wiss. Zool.*, 1867, p. 184.

I do not by any means intend to deny that this is the case. Nevertheless I never found them take any notice of any noise which I made, even when it was close to them. I tried one of my bees with a violin. I made all the noise I could, but to my surprise she took no notice. I could not even see a twitch of the antennæ. The next day I tried the same with another bee, but could not see the slightest sign that she was conscious of the noise. On 31st August I repeated the same experiment with another bee with the same result. On 12th and 13th September I tried several bees with a dog-whistle and a shrill pipe ; but they took no notice whatever, nor did a set of tuning-forks which I tried on a subsequent day have any more effect. These tuning-forks extended over three octaves, beginning with *a* below the ledger line. I also tried with my voice, shouting, etc., close to the head of a bee ; but, in spite of my utmost efforts, the bees took no notice. I repeated these experiments at night when the bees were quiet ; but no noise that I could make seemed to disturb them in the least.

In this respect the results of my observations on bees entirely agreed with those on ants, and I will here, therefore, only refer to what has been said in a preceding chapter (pp. 171–7). Details of some recent experiments are, however, presented here.[56]

On 30th September, 1882, I put out a small quantity of honey on my lawn, and brought some bees to it. I then set a musical box going, and continually replenished the honey and wound up the box. The weather was lovely, and all day a certain number of bees visited the honey.

Then, on 8th October, I removed the honey to an open window on the first floor and set the musical box playing as usual by its side. I waited half an hour, but not a bee came. I need hardly say that the music was quite audible on the lawn. I then again put the musical box and the honey on the lawn, and the bees very soon again began work. After the lapse of an hour I brought the honey and musical box into the house, and placed them at an open drawing-room window less than 15 yards from where they had stood on the lawn. The music was kept going for an hour, but not a bee came.

The following day was again extremely fine. The bees came as usual to the honey. I let them feed till 10 a.m., when I removed the honey as before to the drawing-room. After the lapse of half an hour I set the box playing, and waited half an hour, but not a bee came.

I then put the honey and musical box again out on a chair on the lawn, 5 yards in front of the drawing-room window. The first bee found the honey in $5\frac{1}{4}$ minutes. I left it so for three-quarters of an hour, and then brought the honey and musical box into the house and put them just inside the window but out of sight. The box was kept playing for three-quarters of an hour, during the whole of which a few bees kept hovering round the chair; but not a single bee found the honey, or even was attracted by the music into the room. I then took the honey and put it again on the chair outside. In less than 5 minutes nine bees had settled on it. I then brought it back into the room, and put it, with the bees on it, where it had stood previously. The bees fed, returned to the hive, and came back again to the honey as usual, showing that they had not the slightest objection to enter the house.

I then took the honey and the musical box down to the hives. Immediately (i.e. about a yard) in front of my hives is a low wall; and I put the box and the honey on the far side of the wall, so that they were something less than 4 yards distant from the hive, but of course not directly visible. I then kept the music going for two hours, from 1.30 to 3.30 p.m., but not a bee came to the honey.

From these experiments we are, I think, justified in concluding either that the bees did not hear the music, or that, though they had been feeding close to the music, eight days was not a long enough period to suggest to them that there could possibly be any connection between the honey and the musical box.

To decide between these two alternatives, I moved the musical box (without setting it to play) and honey to another part of the lawn about 15 yards from the first, and put an equal quantity of honey on a similar piece of glass at about the same distance both from the musical box and from the spot where the box had previously been. In half an hour there were several bees at the honey on the musical box, and none at the other. After this we had a week of rain. The next fine morning I again put out the musical box with some honey, and at a distance of about 15 yards a similar quantity of honey on a bit of glass on the grass. In half an hour there were several bees at the honey on the musical box, and none on the other.

I had intended to repeat this several times for greater security, but was unfortunately prevented by bad weather. The observations, however, indicate, as far as they go, that the bees did connect the presence of the musical box with that of the honey, and were guided by it, even if it were not playing, so long as they could see it, but that if they could not see it, even though it were playing, it did not assist them.

The Colour Sense of Bees

The consideration of the causes which have led to the structure and colouring of flowers is one of the most fascinating parts of natural history. Most botanists are now agreed that insects, and especially bees, have played a very important part in the development of flowers.* While in many plants, almost invariably with inconspicuous blossoms, the pollen is carried from flower to flower by the wind, in the case of almost all large and brightly coloured flowers this is effected by the agency of insects.

* See Note 21.—Ed.

In such flowers the colours, scent, and honey serve to attract insects, while the size and form are arranged in such a manner that the insects fertilize them with pollen brought from another plant.

There could, therefore, be little doubt that bees possess a sense of colour. Nevertheless I thought it would be desirable to prove this if possible by actual experiment, which had not yet been done. Accordingly on 12th July I brought a bee to some honey which I placed on blue paper, and about 3 feet off I placed a similar quantity of honey on orange paper. After she had returned twice I transposed the papers; but she returned to the honey on the blue paper. After she had made three more visits, always to the blue paper, I transposed them again, and she again followed the colour, though the honey was left in the same place. The following day I was not able to watch her; but on the 14th at—

7.29 a.m. she returned to the honey on the blue paper. At 7.31 she left.
7.44 ,, ,, ,, 7.41 ,,
7.56 ,, ,,

I then again transposed the papers. At 8.5 she returned to the old place, and was just going to alight; but observing the change of colours, without a moment's hesitation darted off to the blue. No one who saw her at that moment could have entertained the slightest doubt about her perceiving the difference between the two colours. At 8.9 she went.

8.13 she returned to the blue; at 8.16 she left.
8.20 ,, ,, 8.23 ,,
8.26 ,, ,, 8.30 ,,

Transposed the colours again.

At 8.35 she returned to the blue, and at 8.39 left.
8.44 ,, ,, 8.47 ,,
8.50 ,, ,, 8.53 ,,

Transposed the colours again.

8.57	she returned again to the blue ;	9. 0	left
9. 4	,, ,,	9. 7	,,
9.12	,, ,,	9.15	,,
9.19	,, ,,	9.22	,,
9.25	,, ,,	9.27	,,
9.30	,, ,,	9.34	,,
9.40	,, ,,	9.44	,,
9.50	,, ,,	9.55	,,
Transposed the colours again.			
10. 2	she returned again to the blue ;	10. 6	,,
10.10	,, ,,	10.14	,,
10.20	,, ,,	10.25	,,
10.30	,, ,,	10.34	,,
10.40	,, ,,	10.44	,,
10.48	,, ,,	10.51	,,
11.12	,, ,,	11.14	,,
11.21	,, ,,	and flew about, having been disturbed.	
11.26	,, ,,	11.28	left.
11.36	,, ,,	11.40	,,
12. 5	came and flew about, but did not settle till—		
12.17	she returned again to the blue ;	12.17	went.
12.21	came and flew about.		

Though it was a beautiful afternoon, she did not return any more that day.

On 2nd October I placed some honey on slips of glass resting on black, white, yellow, orange, green, blue, and red paper. A bee which was placed on the orange returned twenty times to that slip of glass, only once or twice visiting the others, though I moved the position and also the honey. The next morning again two or three bees paid twenty-one visits to the orange and yellow, and only four to all the other slips of glass. I then moved the glass, after which, out of thirty-two visits, twenty-two were to the orange and yellow. This was due, I believe, to the bee having been placed on the orange at the beginning of the experiment. I do not attribute it to any preference for the orange or yellow ;

indeed, I shall presently give reasons for considering that blue is the favourite colour of bees.

6th October.—I had ranged my colours in a line, with the blue at one end. It was a cold morning, and only one bee came. She had been several times the preceding day, generally to the honey which was on the blue paper. This day also she came to the blue; I moved the blue gradually along the line one stage every half-hour, during which time she paid fifteen visits to the honey, in every case going to that which was on the blue paper.

Again, on 13th September at 11 a.m., I brought up a bee from one of my hives; at 11.40 she returned to honey which I had put on a slip of glass on green paper. She returned at 11.51. And again

At 12. 1
,, 12.13
,, 12.22
,, 12.33
,, 12.46
,, 12.58

She returned at 1.12. This time she lost her way in the room.
,, 1.49
,, 2. 1. This time she got stuck in the honey, and had to clean herself.
,, 2.25
,, 2.40. I now put red paper instead of the green, and put the green paper with a similar quantity of honey on it a foot off.
,, 2.51 to the honey on green paper. I then gently moved the green paper, with the bee on it, back to the old spot. When the bee had gone, I put yellow paper where

the green had been, and put the green again a foot off.

She returned at 3. 0 to the honey on the yellow paper. I disturbed the bee, and she at once flew to the honey on the green paper; when she had gone, I put orange paper in the old place, and put the green paper about a foot off.

,, 3.10 to the honey on the green paper. I again gently moved the paper, with the bee on it, to the usual place; and when the bee had gone, put white paper in the old place, and put the green a foot off.

,, 3.20 to the honey on the green paper. I again gently moved the green paper, with the bee on it, to the old place; and when she had gone, replaced it by blue paper, putting the green a foot off

,, 3.30 to the honey on the green paper. I again repeated the same thing, putting yellow instead of blue.

,, 3.40 to the green paper. I now reversed the position of the yellow and green papers; but

,, 3.51 to the green. After this

,, 4. 6

She returned at 4.15

" 4.28, when she left off for the day, nor were there any bees still working in the garden. The same afternoon a wasp, which I was observing, remained at work till 6.29 p.m.

20th August.—About noon I brought five bees to some honey at my window. They all soon returned, and numerous friends came with them. One of them I put to some honey on blue paper. She returned as follows, viz. :—

At 12.36	At 2.30
" 12.42	" 2.38
" 12.53	" 3. 2
" 1.28	" 3.10
" 1.38	" 3.22
" 1.49	" 3.50
" 2. 2	" 4. 4
" 2.11	" 4.14
" 2.24	" 4.23

when I left off watching and shut her out. The longer intervals are due to her having got some honey every now and then on her wings and legs, when she lost a little time in cleaning herself.

21st August.—I opened my window at 6 a.m. No bee came till at 7.33 the one above mentioned came to the honey on blue paper.

I also placed some honey on orange paper about two feet off.

At 7.42 she returned to the honey on blue paper, and again

" 7.55 she returned to the honey on blue paper.

" 8. 3 " " "

" 8.14 " " "

" 8.25 " " "

" 8.36 " " "

" 8.44 " " "

" 8.54 " " "

" 9. 5 " " "

I then transposed the papers, but not the honey.

At 9.16 she came back to the honey on blue paper. I then transposed the papers again.

At 9.29 she came back to the honey on blue paper. I then transposed them again.

At 9.39 ,, ,, ,,

At 9.53 she came back to the honey on blue paper. I now put green paper instead of orange, and transposed the places.

At 10.0 she came back to the honey on green paper. I transposed them again.

At 10.8 she came back to the honey on blue paper. I transposed them again.

At 10.21 she came back to the honey on green paper. I now put red paper instead of green, and transposed the places.

At 10.30 she came back to the honey on blue paper. I transposed them again.

At 10.42 ,, ,, ,,
,, 10.53 ,, ,, ,,
,, 11. 4 ,, ,, ,,
,, 11.16 ,, ,, ,,

I now put white paper instead of red, and transposed the places.

At 11.28 she came back to the honey on blue paper. I transposed them again.

At 11.41 ,, ,, ,,
,, 11.56 ,, ,, ,,
,, 12. 8 ,, ,, ,,

At 12.17 she came back to the honey on blue paper. I now put green paper again instead of white, and transposed the places.

At 12.27 she came back to the honey on blue paper. I transposed them again.

At 12.40 ,, ,, ,,
,, 12.50 ,, ,, ,,
,, 1. 0 ,, ,, ,,
,, 1.13 ,, ,, ,,

At 1.25 she came back to the honey on blue paper, and then to the green. I transposed them again.

At 1.40 she came back to the honey on blue paper. I transposed them again.

At 1.47 she came back to the honey on green paper.

,, 1.57 she came back to the honey on blue paper, and then to the green.

At 2.6 she came back to the honey on blue paper.

,, 2.17 ,, ,, ,,

The following day I accustomed this bee to green paper. She made 63 visits (beginning at 7.47 and ending at 6.44), of which 50 were to honey on green paper.

The following day, 23rd August, she began work—

At 7.12 returning to honey on green paper. I then put some on yellow paper about a foot off.

At 7.19 she turned to the honey on green paper. I transposed the colours.

At 7.25 she turned to the honey on green paper. I replaced the yellow paper by orange and transposed the places.

At 7.36 she turned to the honey on green paper. I transposed the colours so that the orange might be on the spot to which the bee was most accustomed.

At 7.44 she turned to the honey on green paper. I now put white instead of orange.

At 7.55 she turned to the honey on green paper. Transposed the papers.

At 8.1 she turned to the honey on green paper. I now put blue paper instead of white.

At 8.12 she turned to the honey on blue paper; but it will be remembered that she had been previously accustomed to come to the blue. I now put red instead of blue.

At 8.23 she turned to the honey on green paper.

,, 8.25 ,, ,, ,,

,, 8.47 ,, ,, ,,

I then ceased observing and removed the honey.

Thus the bee which was accustomed to green, returned to that colour when it was removed about a foot, and replaced by yellow, orange, white, and red ; but, on the other hand, when it was replaced by blue, she went to blue. I kept this bee under observation till the 28th, but not with reference to colours.

24th August.—At 7.45 I put another bee to honey on green paper, to which she kept on returning till 9.44. The next day (25th August) she came at 7.38, and I let her come to the green paper till 9. The following morning she returned at 6 a.m., coming back as follows, viz. :—

At 6.10
,, 6.18
,, 6.25
,, 6.35
,, 6.45
,, 6.54
,, 7. 3
,, 7.13

I now put orange in place of green and put the green a foot off.

At 7.24 she returned to the green. I replaced the paper with the bee on it ; and when she had gone I put light blue in place of the green, and again moved the green a foot off.

At 7.36 she returned to the blue. I again replaced the paper with the bee on it ; and when she had gone I put yellow in place of the green, and again moved the green a foot off.

At 7.44 she returned to the green. I then did exactly the same, only putting vermilion in place of the green.

At 7.55 she returned to the green. I then did exactly the same, only putting white in place of green.

At 8.3 she returned to the green.

These observations clearly show that bees possess the power of distinguishing colours.[57]

It remained to determine, if possible, whether they have any preference for one colour over another. M. Bonnier in a recent memoir * denies this. He does not question the power of insects to distinguish colours, which he admits that the preceding observations clearly prove, but he maintains that they would not be in any way attracted or guided by the colours of flowers. This he has attempted to demonstrate by experiment. With this view he proceeded as follows: He took four cubes, 22 cm. by 12 (i.e. about 9 inches by $3\frac{1}{2}$), and coloured red, green, yellow, and white, placing them 6 feet apart in a line parallel to and about 60 feet distant from the hives. He then placed on each an equal quantity of honey, and from minute to minute counted the number of bees on each cube. He found that the number of bees on each was approximately equal, and that the honey was removed from each in about twenty minutes. In the experiment he records the bees began to arrive directly the honey was arranged, and in ten minutes there were nearly a hundred bees on each cube. I presume, therefore, that the bees were previously accustomed to come to the spot in question, expecting to find honey.

I do not think, however, that any conclusive result could be expected from this experiment. In the first place, after the first five minutes there were about thirty bees on each cube, and in less than ten minutes nearly a hundred, and the colour therefore must have been almost covered up. The presence of so many bees would also attract their companions. Moreover, as the honey was all removed in less than twenty minutes, the bees were evidently working against time. They were like the passengers in an express train, turned hurriedly into a refreshment room; and we cannot expect that they would be much influenced by the colouring of the tablecloth. In fact, the experiment was too hurried, and the test not delicate enough.

Then, again, he omitted blue, which I hope to show is the bee's favourite colour, and his cubes were all

* *Les Nectaires.*

coloured. It is true that one was green; but any one may satisfy himself that a piece of green paper on grass is almost as conspicuous as any other colour. To make this experiment complete, M. Bonnier should have placed beside the honey on the coloured cubes a similar supply, without any accompaniment of colour to render it conspicuous.

I could not, therefore, regard these experiments as at all conclusive. The following seem to me a more fair test:—

I took slips of glass of the size generally used for slides for the microscope, viz. 3 inches by 1, and pasted them on slips of paper of the same size, coloured respectively blue, green, orange, red, white, and yellow. I then put them on a lawn, in a row, about a foot apart, and on each put a second slip of glass with a drop of honey. I also put with them a slip of plain glass with a similar drop of honey. I had previously trained a marked bee to come to the place for honey. My plan then was, when the bee returned and had sipped about for a quarter of a minute, to remove the honey, when she flew to another slip. This then I took away, when she went to a third; and so on. In this way—as bees generally suck for three or four minutes—I induced her to visit all the drops successively before returning to the nest. When she had gone to the nest I transposed all the upper glasses with the honey, and also moved the coloured glasses. Thus, as the drop of honey was changed each time, and also the position of the coloured glasses, neither of these could influence the selection by the bee.

In recording the results I marked down successively the order in which the bee went to the different coloured glasses. For instance, in the first journey from the nest, as recorded below, the bee lit first on the blue, which accordingly I marked 1; when the blue was removed, she flew about a little and then lit on the white; when the white was removed, she settled on the green; and so on successively on the orange, yellow, plain, and red.

I repeated the experiment a hundred times, using two different hives—one in Kent and one in Middlesex—and spreading the observations over some time, so as to experiment with different bees, and under varied circumstances. Adding the numbers together, it of course follows that the greater the preference shown for each colour the lower will be the number standing against it.

The following table gives the first day's observations *in extenso* :—

Journeys.	Blue.	Green.	Plain Glass.	Orange.	Red.	White.	Yellow.
1	1	3	6	4	7	2	5
2	5	4	7	6	1	2	3
3	1	4	7	6	5	3	2
4	2	4	6	7	5	1	3
5	1	4	7	2	6	5	3
6	1	2	3	6	5	4	7
7	2	1	4	7	3	5	6
8	3	4	6	2	7	5	1
9	5	1	7	4	6	3	2
10	1	6	7	5	3	2	4
11	4	6	5	2	7	3	1
	26	39	65	51	55	35	37

In the next series of experiments the bees had been trained for three weeks to come to a particular spot on a large lawn, by placing from time to time honey on a piece of plain glass. This naturally gave the plain glass an advantage ; nevertheless, as will be seen, the blue still retained its pre-eminence. It seems hardly necessary to give the observations in detail. The following table shows the general result :—

Series.	No. of Exp.	Blue.	Green.	Orange.	Plain.	Red.	White.	Yellow.
1st .	11	26	39	51	65	55	35	37
2nd, May 30	15	38	57	59	72	66	58	70
3rd July 2	16	44	76	82	73	53	53	67
4th ,, 4	15	43	61	64	80	66	50	56
5th ,, 5	10	36	47	39	40	40	36	42
6th ,, 6	2	2	8	9	10	14	6	7
7th ,, 20	11	33	39	50	47	49	41	49
8th ,, 23	10	31	46	48	52	37	35	31
9th ,, 25	10	22	54	38	52	33	35	46
	100	275	427	440	491	413	349	405

The precautions taken seem to me to have placed the colours on an equal footing; while the number of experiments appears sufficient to give a fair average. It will be observed also that the different series agree well among themselves. The difference between the numbers is certainly striking. Adding together 1, 2, 3, 4, 5, 6, and 7, we get 28 as the total number given by each journey; 100 journeys therefore give, as the table shows, a total of 2,800, which divided by 7 would of course, if no preference were shown, give 400 for each colour. The numbers given, however, are—for the blue only 275, for the white 349, yellow 405, red 413, green 427, orange 440, and plain glass as many as 491.

Another mode of testing the result is to take the percentage in which the bees went respectively to each colour first, second, third, and so on. It will be observed, for instance, that out of a hundred rounds the bees took blue as one of the first three in 74 cases, and one of the last four only in 26 cases; while, on the contrary, they selected the plain as one of the first three only in 25 cases, and one of the last four in 75 cases.

	Blue.	Green.	Orange.	Plain.	Red.	White.	Yellow.
First . .	31	10	11	5	14	19	9
Second .	18	11	13	7	10	21	20
Third . .	25	12	8	13	16	13	13
Fourth .	8	23	15	11	11	12	20
Fifth . .	11	13	15	19	17	16	10
Sixth . .	3	15	22	21	18	12	9
Seventh .	4	16	16	24	14	7	19
	100	100	100	100	100	100	100

I may add that I was by no means prepared for this result.

I may very likely be asked, if blue is the favourite colour of bees, and if bees have had so much to do with the origin of flowers, how is it that there are so few blue ones? I believe the explanation to be that all blue flowers have descended from ancestors in which the flowers were green; or, to speak more precisely, in which the leaves immediately surrounding the stamens and pistil were green; and that they have passed through stages of white or yellow, and generally red, before becoming blue. That all flowers were originally green and inconspicuous, as those of so many plants are still, has, I think, been shown by recent researches, especially those of Darwin, Müller, and Hildebrand.

But what are the considerations which seem to justify us in concluding that blue flowers were formerly yellow or white? Let us consider some of the orders in which blue flowers occur with others of different colours.

For instance, in the Ranunculaceæ,* those with simple open flowers, such as the buttercups and Thalictrums are generally yellow or white. The blue delphiniums and aconites are highly specialized, abnormal forms, and doubtless, therefore, of more recent origin. Among the Caryophyllaceæ the red and purplish species are amongst those with highly specialized flowers, such as *Dianthus* and *Saponaria*, while the simple open flowers, which more nearly represent the ancestral type, such as *Stellaria*, *Cerastium*, etc., are yellow and white.

Take again the Primulaceæ. The open-flowered, honeyless species, such as *Lysimachia* and *Trientalis*, are generally white or yellow; while red, purple, and blue occur principally in the highly specialized species with tubular flowers. The genus *Anagallis* here, however, certainly forms an exception.

Among the violets we find some yellow, some blue species, and Müller considers that the yellow is the original colour. *Viola biflora*, a small, comparatively little specialized fly-flower, is yellow; while the large, long-spurred *V. calcarata*, specially adapted to humblebees is blue. In *V. tricolor*, again, the smaller varieties are whitish-yellow; the larger and more highly developed,

* I take most of the following facts from Müller's admirable work on Alpine Flowers.

blue. *Myosotis versicolor* we know is first yellow and then blue ; and, according to Müller, one variety of *V. tricolor alpestris* is yellow when it first opens, and gradually becomes more and more blue. In this case the individual flower repeats the phases which in past times the ancestors have passed through.

The flowers of one species of Lantana last three days, and, as Fritz Müller first pointed out, are on the first day yellow, on the second day orange, and on the third day purple.

The only other family I will mention is that of the Gentians. Here, also, while the well-known deep blue species have long tubular flowers, specially adapted to bees and butterflies, the yellow *Gentiana lutea* has a simple open flower with exposed honey.

Müller and Hildebrand * have also pointed out that the blue flowers, which, according to this view, are descended from white or yellow ancestors, passing in many cases through a red stage, frequently vary, as if the colours had not had time to fix themselves, and by atavism assume their original colour. Thus *Aquilegia vulgaris, Ajuga Genevensis, Polygala vulgaris, P. comosa, Salvia pratensis, Myosotis alpestris,* and many other blue flowers are often reddish or white ; *Viola calcarata* is normally blue, but occasionally yellow. On the other hand, flowers which are normally white or yellow, rarely, I might almost say never, vary to blue. Moreover, though it is true that there are comparatively few blue flowers, still, if we consider only those in which the honey is concealed, and which are, as we know, specially suited to and frequented by bees and butterflies, we find a larger proportion. Thus, of 150 flowers with concealed honey observed by Müller in the Swiss Alps,† 68 were white or yellow, 52 more or less red, and 30 blue or violet.

However this may be, it seems to me that the preceding experiments show conclusively that bees do prefer one colour to another, and that blue is distinctly their favourite.[58]

* *Die Farben der Blüthen*, p. 26. † *Alpenblumen*, p. 492.

CHAPTER XI

WASPS

I HAVE also made a few experiments with wasps.

So far as their behaviour, when they have discovered a store of food, is concerned, what has been said with reference to bees would apply in the main to wasps also. I will give some of the details in the Appendix,* and here only refer very briefly to some of the experiments.

Experiment 1.—Watched a wasp, which I had accustomed to come to my room for honey, from 9.36 a.m. to 6.25 p.m. She made forty-five visits to the honey, but did not bring a single comrade.

Experiment 2.—The following day this wasp began working—at least, came to my room for the first time at 6.55 a.m., and went on passing backwards and forwards most industriously till 6.17 p.m. She made thirty-eight journeys, and did not bring a single friend.

Experiment 3.—Another wasp was watched from 6.16 a.m. till 6 p.m. She made fifty-one journeys, and during the day five other wasps came to the honey. I do not think she brought them.

Experiment 4.—Another wasp was watched from 10 a.m. to 5.15 p.m.; she made twenty-eight journeys, and brought no friend. This wasp returned the next morning at 6 a.m.

Experiment 5.—A wasp was watched from 11.56 a.m. to 5.36 p.m. She made twenty-three journeys, without bringing a friend.

Experiment 6.—Another wasp between 6.40 a.m. and 5.55 p.m. made sixty journeys, without bringing a friend.

* Omitted in this edition.—ED.

Experiment 7.—Another wasp between 7.25 a.m. and 6.43 p.m. made no less than ninety-four visits to the honey, but did not bring a single friend.

Experiment 8.—I watched a wasp on 19th September. She passed regularly backwards and forwards between the nest and the honey, but during the whole day only one other wasp came of herself to the honey; this wasp returned on the 20th, but not one other. The 21st was a hot day, and there were many wasps about the house; my honey was regularly visited by the two marked wasps, but during the whole day only five others came to it.

22nd September.—Again only one strange wasp came, up to one o'clock.

27th September.—Only one strange wasp came.

2nd and 3rd October.—These days were cold; a few marked bees and wasps came to my honey, but no strangers.

4th October.—Two strangers.

6th October.—Only one stranger.

On these days the honey was watched almost without intermission the whole day, and was more or less regularly visited by the marked bees and wasps.

My experiments, then, in opposition to the statements of Huber and Dujardin, serve to show that wasps and bees do not in all cases convey to one another information as to food which they may have discovered, though I do not doubt that they often do so. Of course, when one wasp has discovered and is visiting a supply of syrup, others are apt to come too; but I believe that in many instances they merely follow one another. If they communicated the fact, considerable numbers would at once make their appearance; but I have not often found this to be the case. The frequent and regular visits which my wasps paid to the honey put out for them, prove that it was very much to their taste; yet few others made their appearance.

These and other observations of the same tendency seem to show that, even if wasps have the power of informing one another when they discover a store of good food, at any rate they do not habitually do so.

On the whole, wasps seem to me more clever in finding their way than bees. I tried wasps with the glass mentioned on p. 213, but they had no difficulty in finding their way out.

My wasps, though courageous, were always on the alert, and easily startled. It was, for instance, more difficult to paint them than the bees; nevertheless, though I tried them with a set of tuning-forks covering three octaves, with a shrill whistle, a pipe, a violin, and my own voice, making in each case the loudest and shrillest sounds in my power, I could see no symptoms in any case that they were conscious of the noise.

The following fact struck me as rather remarkable. One of my wasps smeared her wings with syrup, so that she could not fly. When this happened to a bee, it was only necessary to carry her to the alighting-board, when she was soon cleaned by her comrades. But I did not know where this wasp's nest was, and therefore could not pursue a similar course with her. At first, then, I was afraid that she was doomed. I thought, however, that I would wash her, fully expecting, indeed, to terrify her so much that she would not return again. I therefore caught her, put her in a bottle half full of water, and shook her up well till the honey was washed off. I then transferred her to another bottle, and put her in the sun to dry. When she appeared to have recovered I let her out: she at once flew to her nest, and I never expected to see her again. To my surprise, in thirteen minutes the brave little insect returned as if nothing had happened, and continued her visits to the honey all the afternoon.

This experiment interested me so much that I repeated it with another marked wasp, this time, however, keeping the wasp in the water till she was quite motionless and insensible. When taken out of the water she soon recovered; I fed her; she went quietly away to her nest as usual, and returned after the usual absence. The next morning this wasp was the first to visit the honey.

I was not able to watch any of the above-mentioned wasps for more than a few days, but I kept a specimen of *Polistes gallica* for no less than nine months.

I took her, with her nest, in the Pyrenees, early in May. The nest consisted of about twenty cells, the majority of which contained an egg; but as yet no grubs had been hatched out, and, of course, my wasp was as yet alone in the world.

I had no difficulty in inducing her to feed on my hand; but at first she was shy and nervous. She kept her sting in constant readiness; and once or twice in the train, when the railway officials came for tickets, and I was compelled to hurry her back into her bottle, she stung me slightly—I think, however, entirely from fright.

Gradually she became quite used to me, and when I took her on my hand apparently expected to be fed. She even allowed me to stroke her without any appearance of fear, and for some months I never saw her sting.

When the cold weather came on she fell into a drowsy state, and I began to hope she would hibernate and survive the winter. I kept her in a dark place, but watched her carefully, and fed her if ever she seemed at all restless.

She came out occasionally, and seemed as well as usual till near the end of February, when one day I observed she had nearly lost the use of her antennæ, though the rest of the body was as usual. She would take no food. Next day I tried again to feed her; but the head seemed dead, though she could still move her legs, wings, and abdomen. The following day I offered her food for the last time; but both head and thorax were dead or paralysed; she could but move her tail, a last token, as I could almost fancy, of gratitude and affection. As far as I could judge, her death was quite painless; and she now occupies a place in the British Museum.

Power of distinguishing Colours

As regards colours, I satisfied myself that wasps are capable of distinguishing colour, though they do not seem so much guided by it as bees are.

25th July.—At 7 a.m. I marked a common worker wasp (*Vespa vulgaris*), and placed her to some honey on a piece of green paper 7 inches by 4½. She worked with great industry. After she had got well used to the green paper I moved it 18 inches off, putting some other honey on blue paper where the green had previously been. She returned to the blue. I then replaced the green paper for an hour, during which she visited it several times, after which I moved it 18 inches, as before, and put brick-red paper in its place. She returned to the brick-red paper. But although this experiment indicates that this wasp was less strongly affected by colours than the bees which I had previously observed, still I satisfied myself that she was not colour-blind.

I moved the green paper slightly and put the honey, which, as before, was on a slip of plain glass, about four feet off. She came back and lit on the green paper, but finding no honey, rose again, and hawked about in search of it. After 90 seconds I put the green paper under the honey, and in 15 seconds she found it. I then, while she was absent at the nest moved both the honey and the paper about a foot from their previous positions, and placed them about a foot apart. She returned as usual, hovered over the paper, lit on it, rose again, flew about for a few seconds, lit again on the paper, and again rose. After 2 minutes had elapsed I slipped the paper under the honey, when she almost immediately (within 5 seconds) lit on it. It seems obvious, therefore, that she could see green.

I then tried her with red. I placed the honey on brick-red paper, and left her for an hour, from 5 p.m. to

6, to get accustomed to it. During this time she continued her usual visits. I then put the honey and the coloured paper about a foot apart; she returned first to the paper and then to the honey. I then transposed the honey and the paper. This seemed to puzzle her. She returned to the paper, but did not settle. After she had hawked about for 100 seconds I put the honey on the red paper, when she settled on it at once. I then put the paper and the honey again 18 inches apart. As before, she returned first to the paper, but almost immediately went to the honey. In a similar manner I satisfied myself that she could see yellow.

Again, on 18th August I experimented on two wasps, one of which had been coming more or less regularly to some honey on yellow paper for four days, the other for twelve—coming, that is to say, for several days, the whole day long, and on all the others, with two or three exceptions, for at least three hours in the day. Both, therefore, had got well used to the yellow paper. I then put blue paper where the yellow had been, and put the yellow paper with some honey on it about a foot off. Both the wasps returned to the honey on the blue paper. I then moved both the papers about a foot, but so that the blue was somewhat nearer the original position. Both again returned to the blue. I then transposed the colours, and they both returned to the yellow.

Very similar results were given by the wasp watched on 11th September. After she had made twenty visits to honey on blue paper, I put it on yellow paper, and moved the blue 12 inches off. She came back to the yellow. I then put vermilion instead of yellow; she came back to the vermilion. I transposed the colours; she came back to the vermilion.

I put white instead of vermilion; she came to the blue.
,, green ,, white; she came to the blue.
,, orange ,, green; she came to the blue.
I transposed the colours; she returned to the orange.

I put white instead of orange ; she came to the white.
,, green ,, white ; she came to the blue.
,, purple ,, green ; she came to the purple.
,, orange ,, purple ; she came to the orange.
,, green ,, orange ; she came to the green.
I transposed the colours ; she came to the blue.
,, ,, ,, ,, ,, green.

So far, therefore, she certainly showed no special predilection for the blue. I then left her the rest of the day to visit the honey on blue paper exclusively. She made fifty-eight visits to it. The following morning I opened my window at 6.15, when she immediately made her appearance.

I let her make ten more visits to the honey on blue paper, moving it about a foot or so backwards and forwards on the table. I then put orange paper instead of the blue, and put the blue about a foot off. She returned to the orange.

I put yellow instead of orange ; she came to the yellow.
,, vermilion ,, yellow; she came to the vermilion.
,, white ,, vermilion ; she came to the white.
,, green ,, white ; she came to the green.
I transposed the colours ; she came to the blue.

I now put vermilion instead of green, and moved both of them a foot, but so that the vermilion was nearest the window, though touching the blue ; she came to the vermilion.

Again, 11th September, I marked a wasp. She returned to the honey over and over again with the usual assiduity. The following morning I put the honey on green paper ; she came backwards and forwards all day. On the 13th I opened my window at 6.8 and she came in immediately. During an hour she made ten journeys. On her leaving the honey for the eleventh time, I placed some honey on vermilion paper where the green had been, and put the honey and the green paper about a foot off.

She came at 7.25 to the vermilion. I then put orange instead of vermilion.
,, 7.34 ,, orange. I then put blue instead of orange.
,, 7.40 ,, blue. I then put white instead of blue.
,, 7.47 ,, white. I then put yellow instead of white.
,, 7.55 ,, yellow and then to the green. I transposed the colours.
,, 8. 2 ,, green. I then moved both colours about a foot, but so that the yellow was a little nearer to the old place.

She returned at 8.9 to the yellow.

I then removed the yellow paper and honey, and placed the honey which had been on the green paper about a foot from it on the table.

At 8.15 she returned and lit on the green paper, but immediately flew off to the honey. I then transposed the honey and the paper.

At 8.24 she returned and again lit on the paper, but immediately flew off to the honey.

Thus, therefore, though it is clear that wasps can distinguish colours, they appear, as might be expected from other considerations, to be less guided by them than is the case with bees.*

I have been much struck by the industry of wasps. They commence work early in the morning, and do not leave off till dusk. I have several times watched a wasp the whole day, and from morning to evening, if not disturbed, they worked without any interval for rest or refreshment.

Being anxious to compare bees and wasps in this respect, on 6th August, 1882, I accustomed a wasp and three bees to come to some honey put out for them on two tables, one allotted to the wasp, the other to the bees. The last bee came at 7.15 p.m. The wasp continued

* See also Note 57.—Ed.

working regularly till 7.47, coming at intervals of between six and seven minutes. Next morning, when I went into my study a few minutes after 4 a.m., I found the wasp already at the honey. The first bee came at 5.45, the second at 6.

The wasp occupied about a minute, or even less, in supplying herself with a load of honey, and made during the day, as shown in the Appendix * no less than 116 visits to the honey, or 232 journeys between my room and her nest, during which she carried off rather more than sixty-four grains of honey.

It would, however, perhaps be unfair to the bees to regard this as indicating that they are less industrious than wasps. The deficiency may be due to their being more susceptible to cold.

I may add that I then left home for a few days. I covered over the honey, leaving only a small entrance for the wasp. When I returned on the 12th, I found her still at work, and by herself. It was evident that she had continued her labours, but without bringing any friends to assist her.

Everyone has heard of a "bee-line". It would be no less correct to talk of a wasp-line. On 6th August I marked a wasp, the nest of which was round the corner of the house, so that her direct way home was not out of the window by which she entered, but in the opposite direction, across the room to a window which was closed. I watched her for some hours, during which time she constantly went to the closed window, and lost much time in buzzing about at it. 7th August, I was not able to watch her. 8th and 9th August, I watched her from 6.25 a.m., when she made her first visit. She still constantly went to the closed window. 10th and 11th August, I was away from home. 12th August, she made her first visit at 7.40, and still went to the closed window. 13th August, her first visit was at 6.15; she went to the closed window and remained buzzing about there till

* [In earlier edition.]

7, when I caught her and put her out at the open one by which she always entered. 15th and 16th August, she continued to visit the honey, but still, always, even after ten day's experience, continued to go to the closed window, which was in the direct line home; though on finding it closed she returned and went round through the open window by which she entered.[59]

ANNOTATIONS

Note 1 (see also notes 43 and 44).—In the form in which Lubbock expresses it, the ants' "claim to rank next to man in the scale of intelligence" cannot be admitted by modern psychology. In a sense, of course, Lubbock is right, and the divergence only a matter of definitions, for social life "implies a shifting of proclivities from the egocentric to the sociocentric plane through a remarkable increase in the amplitude and precision of the individual's responses to all the normal environmental stimuli"; (Wheeler), and in this respect ants are undoubtedly second only to man. It is true also that we no longer subscribe to the Bergsonian conception of "instinct" and "intelligence" as two utterly divergent developments of mind, the first culminating in the social insects and the second in man. We are willing to credit the insects with much more intelligence, in the sense of plastic behaviour, discrimination or "estimative power"; while the concept of "instinct" whether in animals or men, has become so confused that it seems safer, with Wheeler (1928, p. 226), wherever possible, to avoid the term.

When Lubbock wrote we knew practically nothing of the mentality of the higher apes. It now seems incontrovertible that in individual intelligence as in bodily structure these animals rank next to man. We can best compare their psychic qualities with those of ants by contrasting two quotations. The first, from Lubbock (p. 188), concerns ants. ". . . I suspended some honey over a nest of *Lasius flavus* at a height of about $\frac{1}{2}$ an inch, and accessible only by a paper bridge more than 10 feet long. Under the glass I then placed a small heap of earth. The ants soon swarmed over the earth on to the glass, and began feeding on the honey. I then removed a little of the earth, so that there was an interval of about $\frac{1}{3}$ of an inch between the glass and the earth; but though the distance was so small, they would not jump down, but preferred to go round by the long bridge. They tried in vain to stretch up from the earth to the glass, which, however, was just out of their reach, though they could touch it with their antennæ ; but it did not occur to them to heap the earth up a little, though if they had moved only half a dozen particles of earth they would have secured for themselves direct access to the food. This, however, never occurred to them. At length they gave up all attempts to reach to the glass, and went round by the paper bridge. I left the arrangement for several weeks, but they continued to go round by the long paper bridge."

The second quotation concerns chimpanzees. Köhler * writes : " When the objective [some bananas] is fastened *at a height* from the ground, and unobtainable by any circuitous routes, the distance can be cancelled by means of a raised platform or box or steps which can be mounted by the animals. . . . The six young animals of the station colony were enclosed in a room with perfectly smooth walls, whose roof—about two metres in height—they could not reach. A wooden box (dimensions fifty centimetres by forty by thirty), open on one side, was standing about in the middle of the room, the one open side vertical, and in plain sight. The objective was nailed to the roof in a corner, about two and a half metres distant from the box. All six apes vainly endeavoured to reach the fruit by leaping up from the ground. Sultan soon relinquished this attempt, paced restlessly up and down, suddenly stood still in front of the box, seized it, tipped it hastily straight towards the objective, but began to climb upon it at a (horizontal) distance of half a metre, and springing upwards with all his force, tore down the banana. About five minutes had elapsed since the fastening of the fruit ; from the momentary pause before the box to the first bite into the banana, only a few seconds elapsed, a perfectly continuous action after the first hesitation. Up to that instant none of the animals had taken any notice of the box ; they were all far too intent on the objective ; none of the other five took any part in carrying the box ; Sultan performed the feat single-handed in a few seconds. The observer watched this experiment through the grating from the outside of the cage."

Innumerable examples of this kind and of a more complicated nature, such as piling up four boxes, one on another, the fitting together of two sticks to make a longer one and so

* *The Mentality of Apes*, 2nd ed., London, 1927, p. 39.

on, have led Köhler and also Yerkes to credit the anthropoid apes with " insight ". There are, of course, some instances of tool-using among insects, either as regular behaviour in certain species (spinning ants), or as special performances of gifted individuals (*Ammophila*, a digger wasp, using a stone to pat down the loose earth of her burrow).

NOTE 2.—No myrmecologist of note now considers the ants to form more than a single well-defined family. The progress of taxonomic research, especially in the swarming ant-faunas of the tropics of both hemispheres, has, however, led to the recognition of more sub-families than were necessary for the classification of the ants known to the older workers. Emery and Forel divided the family Formicidæ into five such sub-families, the Ponerinæ, Dorylinæ, Myrmicinæ, Dolichoderinæ, and Formicinæ (Camponotinæ). But Wheeler, to whose recent work (1928, pp. 105–8) the interested reader should turn for the latest and most authoritative treatment of the problem, finds it now necessary to recognize eight, which are as follows: Dorylinæ, Cerapachyinæ, Ponerinæ, Leptanillinæ, Pseudomyrminæ, Myrmicinæ, Dolichoderinæ, Formicinæ. Of these, the Myrmicinæ and Formicinæ are cosmopolitan, and contain most of the ants of Europe and North America, while the members of the other six sub-families are very largely confined to tropical and subtropical lands.

It is still a moot point whether the ants of to-day have descended from several different ancestors, i.e. are polyphyletic, or from one common form. Emery was of the former opinion, but Wheeler and Forel consider that the bulk of the evidence favours the second hypothesis.

A key to all the genera of ants will be found in Wheeler's great work on Congo ants (1922).

NOTE 3.—The growth of myrmecology since Lubbock's day is indicated by the fact that at the present time no fewer than approximately 3,500 species or 6,000 different kinds (species, sub-species, and varieties—Wheeler, 1928, p. 105) of ants have been described. This great increment has been due largely to the exploration of the tropics—an examination which, at least so far as the cryptozoic forms are concerned, has nowhere more than merely scratched the surface. Wheeler estimates that 4,000 more forms of ants will be discovered before the close of the present century.

NOTE 4.—The following is Lubbock's own note (pp. 419–20 of Appendix G in the seventeenth edition) on artificial nests :—

DOMESTIC ECONOMY OF ANTS.

Lastly I give two illustrations which will convey an idea of some of my ant-nests.

Plate V represents about a quarter of one of my frames. The shaded part represents the earth, which will be seen to have been arranged by the ants into a sort of circular fortification, or zereba, access to which is obtained by one or two tunnels, not visible in the illustration, and to which a pathway leads from the entrance.

Plate VI represents a nest of *Lasius niger*. It shows the entrance, vestibule, and two chambers, in the outer and larger one of which the ants have left some pillars, almost as if to support the roof. The queen is surrounded by workers, those in her immediate neighbourhood all having their faces turned towards her. There is a group of pupæ, and several of larvæ, sorted as usual according to ages. There are also a number of the blind woodlice (*Platyarthrus hoffmanseggii*), and of the small *Cyphodeirus albinos*, both of which habitually live in ants' nests.

EDITOR'S NOTE.—Very many types of artificial nests are now used in the study of ants. As a detailed guide to their construction is readily accessible in the larger works of Wheeler (1910, Appendix A), and of Forel (1928, i, pp. 379–91), it will be sufficient here to describe briefly a few of the simpler and more useful.

The Lubbock nest has been modified in a number of ways, and is still widely used.

The apparatus invented by Janet "consists of an oblong block of coloured plaster of paris, containing a series of disk-like depressions in its upper portion. One of these, isolated at the end of the series, is smaller than the others, and is used as a water reservoir, the others, which are inhabited by the ants, are connected with one another by short galleries, and are covered with glass plates and in part also with opaque covers. The water diffuses from the reservoir through the porous plaster block in such a manner that there is a gradation of moisture in the different chambers. This permits the ants to station themselves and their brood at the spot where the conditions are most favourable." (Wheeler, loc. cit.)

The Fielde nest, or a modified form thereof, has a floor of thick glass or of sheet aluminium, on which are securely glued double strips of glass to form the outer walls and partitions. The latter, to provide passage way between the compartments, do not extend right across the nest. The edge of the floor pane and the outside of the walls are bound with cloth. Both the walls and the partitions are then topped with strips of Turkish towelling, which, strongly glued, admit air and prevent the ants escaping between the roof and its supports. The nest now consists of a series of intercommunicating shallow rooms. Each room is covered by a separate sheet of glass, which merely lies on the towelling strips or may be kept in place by elastic bands. The space between roof and floor should be under ½ in. When not under observation, all the rooms save one are covered with black paper, the exception being used as a feeding-chamber. The living rooms may be kept moist enough by a small piece of sponge, wetted once a week, and any chamber which requires cleaning may be emptied of ants by exposing its roof to the light, when its inmates will retire to the darker ones. A great advantage of the Fielde nest is its lightness and ready portability.

Wheeler (1910, p. 554) recommends " a combination of the Janet and Fielde nests. The glass base and sides of the latter are replaced by a single thin block of coloured plaster of paris, but the height and arrangement of the chambers, their communications, the towelling and roof-panes are those of the Fielde nest ".

Santschi uses a special nest for very small ants. " It is quickly constructed merely with wet plaster of paris and glass plates, such as those used in photography. On to the surface of a plate of the required dimensions the plaster is poured in the form of the walls of two oblong or square chambers and a short connecting gallery. Then another plate of the same dimensions, with its surface oiled, is pressed down somewhat on to the plaster before it sets, leaving a space of a few millimetres between the two plates. As soon as the plaster has set, the upper plate is removed and may be cut into two pieces to serve as the covers of the chambers. The plaster is sufficiently porous to admit the air, and the walls leave no spaces for the escape of the ants. This nest is so shallow that it can be placed on the stage of the compound microscope and its inhabitants studied under a low objective." (Wheeler, loc. cit.)

Details of much more complicated nests will be found in the writings of Brun, Kutter, Meldahl, and Wasmann, or in summary, in the work of Forel (loc. cit.).

Finally, Wheeler's warning should be borne in mind that "all of the various artificial nests here described have both admirable qualities and serious defects, so that anyone who wishes to gain a thorough knowledge of the ants will do well not to pin his faith to anyone of them, but will select the form best adapted to the special problem in hand".

Of the methods for inducing ants to enter a new nest and carry in their brood, the Forel arena is probably the most convenient, and may be described in Wheeler's words: "On a table or large board a circular or elliptical enclosure a few feet in diameter is made by laying down a wall of dry, powdered plaster of paris about two or three inches broad and an inch high. The inner edge of this wall is made smooth and steep with the aid of a putty or case-knife. The artificial nest, with its chambers moistened and darkened, is placed in this arena. Then the colony to be installed, together with its brood and the earth of its nest, is dumped from the collecting bag into the arena just as it was brought in from the field. The ants are at first much excited and wander about in the enclosure, but are unable to scale its crumbling walls. They soon learn to avoid the powdery plaster, find the entrance of the nest, and migrate into it with their whole brood and any myrmecophiles they may have. This migration is hastened by spreading out the earth from their old nest so that it may dry. When the colony has entered, the nest opening is plugged with cotton, and the nest is removed from the arena. Small colonies or colonies of small and delicate species, which, as I have said, are best collected in bottles plugged with cotton, may be hastily poured directly into one of the chambers of the nest. By illuminating this chamber the ants may be induced to move into the adjoining dark chamber and the fragments of the original nest can then be removed." (Wheeler, loc cit., p. 556.)

Note 5.—One of the most interesting discoveries which the study of ant biology has yielded since Lubbock's time concerns the relation between ants and their larvæ in general, and the structure and treatment of the larvæ in a certain sub-family, the Pseudomyrminæ, in particular. The latter formed the subject of a paper (1918) in which Wheeler brought forward the concept of "trophallaxis" or exchange of food. (See also Wheeler, 1928, chap. ix.) It was already known that many social wasp larvæ secrete drops of saliva which are eagerly lapped up by the workers which feed them. Termites feed one another to such an extent that the members of a colony "may be said to be bound together by a circulating medium of glandular secretions, fatty exudates and partly and wholly digested food, just as the cells of the body of a higher animal are bound together as a syntrophic whole by means of the circulating blood". (Wheeler, 1923, p. 260.) Adult ants are well known to share food, but this exchange reaches a bizarre extreme in the larvæ of the Pseudomyrminæ. In these, the mouth of the younger larvæ is surrounded by long slender papillæ or exudatoria producing a secretion greedily sought by the nurses, which in return feed their charges on little more than rubbish—in other words, with the pellets of foreign matter and secretions cleaned off the adults' bodies and stored in the infrabuccal pocket. It remained for Wheeler to stress the significance of the fact that the more typical ant-larvæ also are licked by the workers, which in addition lick one another and the queen, while the queen licks her original brood; to show that a more or less complete exchange of a similar kind takes place between ants, their guests and their "cows"; and finally to co-ordinate these observations in the concept of "trophallaxis" as a key to the understanding of social behaviour among the insects. More recently (Wheeler, 1928, pp. 239–45) the scope of the principle has been extended "to cover an even greater number of phenomena, if we include besides the substances that are socially excitatory through the taste receptors also those that affect the other chemical sense, namely olfaction", which, in insect physiology, can hardly be clearly differentiated from taste. The essence of the theory lies in the excitatory rather than the nutritive value of the exchange.

It is true that reciprocal feeding of nurses and larvæ, and thus trophallaxis in the narrowest sense, has not yet been demonstrated in any social bees, but it is by no means improbable that such may eventually be found to occur. In ants, wasps, and termites it is unquestionably of the highest social significance.

The greatest critic of the trophallactic hypothesis has been Wasmann (1920, 1923), who, basing his psychology on the scholastic philosophy, would attribute the behaviour of ants towards their brood and towards various guests to so many specific instincts.

NOTE 6.—Not only do the nurses help out of their cocoons the *callows* or still soft adult ants, but they also strip the pupal skin from those kinds in which a cocoon is absent, and at an earlier stage remove the meconium, or accumulated digestive residues of larval life, sometimes even pulling it directly out of the rectum (Wheeler).

While it is thus true that the services of the workers to the emerging adults are extremely intimate, yet according to Forel and to Donisthorpe (1927*a*, p. 34), the lack of this assistance is not, as Lubbock believed, always fatal.

Thus Forel found that workers, but not males, of *Tetramorium cæspitum*, could emerge entirely unaided. He "then repeated the experiment with ☿ nymphs of *Formica pratensis*, which were then ready to hatch, and the ♀ nymph of an amazon ant which I had myself extracted most carefully from their cocoons. And every one of them was able to come out of the pupal skin unaided; even the ♀ amazon, which managed on her own account to spread and entirely free her wings and the extremity of the abdomen. . . . The ♀ ant, then, at any rate, is capable of dispensing with the aid of its companions in coming out of the pupal skin. On another occasion I made a counter experiment by enclosing in a box, in the same way, ☿, ♀, and ♂ cocoons of many diverse species of the genus *Formica*, shortly before their hatching time. All the nymphs inside perished without being able to hatch, in contradistinction to what took place in the experiment with the Ponerinæ (see below). In this respect, then, Pierre Huber was right. . . . What is true in one place for the one creature is false in another place for the other creature." (Forel, 1928, i, pp. 28, 29.)

In the sub-family Ponerinæ, as shown by Wheeler, the callows emerge unaided from their cocoons. This is what we should expect in view of the primitive nature of these ants, and it was indeed predicted by Forel. Incidentally the Ponerinæ supply a refutation to Lubbock's statement (p. 7) that "as a general rule the species which have not a sting are enveloped in a cocoon, while those which have are naked"; for these ants are furnished with powerful stings but spin cocoons.

NOTE 7.—The following is Lubbock's own note (pp. 415–16 of Appendix G in the seventeenth edition) on this question :—

LONGEVITY.

It may be remembered that my nests have enabled me to keep ants under observation for long periods, and that I have identified workers of *Lasius niger* and *Formica fusca* which were at least seven years old, and two queens of *Formica usca* which have lived with me ever since December, 1874. One of these queens, after ailing for some days, died on 30th July, 1887. She then must have been more than thirteen years old. I was at first afraid that the other one might be affected by the death of her companion. She lived, however, until 8th August, 1888, when she must have been nearly fifteen years old, and is, therefore, by far the oldest insect on record.

Moreover, what is very extraordinary, she continued to lay fertile eggs. Fertilization took place in 1874 at the latest. There has been no male in the nest since then, and, moreover, it is, I believe, well established that queen ants and queen bees are fertilized once for all. The continued fertility of this queen ant is therefore most remarkable, and very interesting from a physiological point of view.

In some plants (Rues) the pollen-tube takes as long as two years to reach the ovule. Indeed, the pollen has some claims to be regarded as a separate organism, for it certainly possesses the power of growth, and of assimilating nourishment. There is not, however, so far as I am aware, any other case which can compare with this of my queen ant.

Moreover, the case is not altogether isolated. I had another queen of *Formica fusca* which lived to be thirteen years old, and I have now a queen of *Lasius niger* which is more than nine years old and still lays fertile eggs which produce female ants.

EDITOR'S NOTE.—Lubbock's record age of fifteen years for one of his queen ants seems still to be unbeaten, while few observers have been able to keep males or workers for as long as he did. His claim, however, that the above queen is the oldest insect on record is unfounded. The famous periodical cicada (*Magicicada septendecim*) of North America regularly takes seventeen years to complete its life-cycle—most of which is passed underground—and there is considerable evidence that other species of cicadas may live even longer.

Ferris * records a Coccid (*Margarodes vitium*) from Chile, which lived in an encysted state in a collection of dried insects for no less than seventeen years.

The familiar instance of a mayfly (Ephemeridæ), which spends three years in the pre-adult stages is mentioned by Berlese,† who cites also Marsham's Buprestid beetle, which was seen to emerge from the wood of a desk kept for twenty years in a government office. The insect must have passed this time in the wood as a larva and pupa. Warnenburg is said to have kept in captivity a cellar-beetle—*Blaps gigas*—as an adult, for nearly ten years (3,349 days).

NOTE 8.—Lubbock's description is morphologically misleading, for studies of ant-development have shown that the first abdominal segment of the larva is fused with the thorax in the later stages. The true second abdominal segment (Formicinæ, Dolichoderinæ) or the second and third together (Myrmicinæ) form a petiole, while the remainder, forming the typically oval greater part of the abdomen, constitute the "gaster" of myrmecologists.

NOTE 9.—Modern research strongly supports Lubbock's view that ants are descended from forms with a well-developed sting, "and that the rudimentary [or rather vestigial] condition of that of *Formica* is due to atrophy . . ." The Ponerinæ, recognized as the most primitive of living ants, are furnished with a powerful sting, which, in those especially archaic forms, the bull-dog ants (*Myrmecia*) of Australia, becomes a really terrifying weapon.

NOTE 10.—Lubbock does not describe the curious shape of the head in those forms which use it for stopping up circular nest-entrances. In the soldier caste of the sub-genus *Colobopsis*,

* A remarkable case of longevity in insects. *Ent. News*, vol. xxx: pp. 27–8.

† *Gli Insetti*, vol. ii: p. 766.

this door-keeping head is truncate and quite circular, to fit the opening exactly. A similar adaptation exists in at least four other ant genera, and among other Arthropods, in some of which it is the posterior end of the body which is thus comically modified into a plug. There are even certain West Indian toads and frogs which stop their burrows with their hard, exactly-fitting heads. This curious phenomenon, in which an actual part of the body, either fore or hind, is made into a door, has been termed *phragmosis* by Wheeler (1928, pp. 188–90), who points out the interesting correlation it involves " between behavioristic activities on the one hand and physiological and morphogenic processes on the other ".

Note 11.—A special type of huge workers, with extremely large heads, occurs in many species of ants. These are the so-called " soldiers " or *dinergates* of Wheeler. Their function is still not in all cases clear. Forel points out (1928, i, p. 33) that the small worker " is occupied in work inside the nest, and in its external defence and the search for food ", while the large worker " is differentiated in the first place for certain work which demands more strength, and also partly for defence ". Nevertheless, it is the small worker, as Forel himself points out (loc. cit., p. 34) which is, for most of the time, the real defender of the nest. The largest workers or soldiers of *Pheidologeton* and *Pheidole, Messor, Novomessor,* and *Holcomyrmex* grind up seeds with their huge mandibles and cut up insects and similar food into small pieces (Forel, Wheeler).

In the case of the leaf-cutting ants (Atta) mentioned by Lubbock, " the maximæ, or soldiers, guard the nest." (Wheeler, 1910, p. 337.)

Finally, " in many species of *Pheidole, Pheidologeton,* and *Oligomyrmex,* the soldiers may act as honey-pots . . ." (Wheeler, 1928, p. 235.) (See also Note 20.)

Note 12.—The problem of the origin of castes in the social insects has exercised the wits of biologists since long before the days of Lubbock, and is likely still to baffle them for as long again. In the last analysis the puzzle really resolves itself into the old argument between predetermination and epigenesis, and thus epitomizes a conflict of attitude which has long divided biologists—and philosophers—into two camps.

The differentiation of female ants and other social insects into separate castes occurs within the highly complex environment of the nest or colony. But the factors of such environment, all save one, exert their influence practically alike on all the members of the community. The exception is the nutricial factor, for the method of feeding is known to vary between the different castes. If, then, the formation of castes is not predetermined in the egg, it must be produced by differential feeding. Even with this simplification, however, the problem remains exceedingly complicated, and we are faced with five main possibilities :—

(1) The eggs are all alike, and the different castes are produced by feeding. This is the view usually held by students of bees.

(2) The eggs are intrinsically different, and each caste develops from a different kind of egg. Feeding at most only influences stature.

(3) The eggs are all alike, but each has either a definite nuclear structure, which responds to special food, to produce a specific caste ; or differential potentialities which may react specifically to a particular kind of food.

(4) The castes may be predetermined in some groups of social insects and produced by feeding in others.

(5) Some of the castes in a given species may be predetermined, while others are caused by differential feeding.

What is the evidence for these various theories among the different groups of social insects ? Wheeler (1928, chapter viii) has recently reviewed the whole subject in a most illuminating chapter of which this note is a very brief digest.

In the social wasps, and similarly in the humble-bees, where caste differences are but slight, they have been, in all probability, brought about solely by differences in the quantity of the food supplied to the larvæ. In the hive bee there is no doubt that qualitative differences in feeding come into play. It has been shown repeatedly that an egg or young larva taken from a worker cell and placed in a queen cell, where it is fed with " royal jelly " or saliva, becomes a queen bee.

In ants the question becomes greatly involved in consequence of the extreme variety of food material, and the evidence available is largely indirect. The interested reader should consult Wheeler's account (loc. cit.).

The first to concern himself with the problem in termites was Grassi, who became convinced that the eggs are all similarly constituted, and that the castes result solely from differential feeding. Many of the most experienced students of termites (Feytaud, Heath, Escherich, Jucci) have shared Grassi's views. Other workers (Bugnion, Miss Thompson, Snyder, Imms), however, claim that the different castes of termites are distinguishable, either in external or internal structure—at hatching, and that even further development depends upon innate factors uninfluenced by the environment. They have suggested that we are in the presence of a Mendelian phenomenon; but their theory remains to be proved by experiment, while their morphological data have been seriously questioned.

Thus in the oldest and most highly organized of insect societies—those of the ants and of the termites—the problem of the origin of castes is still *sub judice.* In these two groups it is not to be expected that future investigation will provide any all-embracing solution in terms of either of the rival hypotheses. Rather may we anticipate a compromise on the lines of possibilities (4) and (5) above. In a final paragraph which we feel impelled to quote, Wheeler (1928, pp. 221–2) has well shown the difficulties in both of the two simpler original theories: "It has been suggested that the production of workers and soldiers in the colony is a kind of experimental teratogeny carried on by the worker nurses, but it is certainly strange that the monsters produced, e.g. the janitor soldiers of Colobopsis among the ants and the nasuti among the termites, should be structurally and functionally so exquisitely adapted to their particular professions. And it strains our credulity to be told that such forms arise either from peculiar genes popping out of nowhere into the germ plasm or develop gradually under the guidance of natural selection from forms which, so far as we can see, must have an equal or even greater survival value. When we encounter such *impasses* as the foregoing, instead of embracing the Aristotelian Entelecheia, that belldame of more than two thousand summers, now so popular on the other side of the Rhine, or joining the apostles of the survival of the fittest and forever croaking 'natural selection!' it is surely more commendable to sit down in the laboratory or in the field and say nothing but '*ignoramus*' till we have made a much more exhaustive behaviouristic and physiological investigation of the phenomena. '*Nullus* sermo in his potest certificare, totum enim dependet ab experimentiâ.' (Roger Bacon.)"

NOTE 13.—There is no doubt that the relations between ants and their milch cows, whether these latter be aphides, scale-insects, or tree-hoppers, are truly symbiotic—that is, both parties reap considerable benefit from the association. The protection afforded by those ants which build carton "stables" for their cattle, collect and tend their eggs and so on, has been sufficiently and clearly established. So powerful has this protection become in certain cases, that the control of many extremely destructive plant-lice and scale-insects, including the corn-root aphis (*Aphis maidiradicis*) in North America (Forbes), the coffee mealy-bug (*Pseudococcus lilacinus*) in Kenya (Kirkpatrick), and a banana mealy-bug (*Pseudococcus comstocki*) in the Canaries (Wheeler, MacDougall), has become purely a matter of controlling the host-ants. Destroy the ants or prevent their access to the infested plants and the aphides or Coccids in question soon become negligible as pests.

It is, however, by no means easy to analyse the nature of the favourable influence exercised by the ants.* Thus Green found that the silken shelters constructed over the soft scale (*Lecanium hemisphæricum*) by the tree-ant (*Œcophylla smaragdina*) offer no security against Braconid parasites nor against the attacks of a carnivorous caterpillar (*Eublemma*). These shelters, however, as I have seen in Ceylon, are very flimsy and not comparable in strength of texture either with those built for the ant-brood itself, or with the carton stables built by other ants.

What measure of active protection is conferred by those ants which merely milk their animals in the open is still less certain. Wheeler (1910) believes that at least predatory enemies are driven off. Büsgen found that the cornicles of aphides—dorsal abdominal tubes which were long quite erroneously believed to secrete honey-dew—in reality exude

* For a discussion of this problem, see a paper by the present writer on "Insect exploiters of animal secretions", in the *Bulletin of the Brooklyn Entomological Society*, 1928, where full citations of the literature will be found. Only citations not included in that paper are given here.

a more or less viscid substance which is discharged, as a defensive measure, on the face and jaws of predacious insects like aphis-lions (*Chrysopa*) and ladybird larvæ. Now Mordwilko (quoted by Wheeler, 1910, p. 346) showed that these cornicles or "siphons' are best developed in certain species of Aphididæ that live singly and not in droves or colonies and are not attended by ants, whereas these repugnatorial glands may be vestigial or completely lacking in the species thus attended. This is certainly suggestive of their great importance as organs of defence".

The evidence for active protection is by no means copious. Büsgen in his important treatise on honey-dew, claims to have seen the ants drive aphis-lions (*Chrysopa* larvæ) off their preserves, and Ferton * writing of the ant, *Tapinoma erraticum* and its aphides, says: "While observing the aphid-hunting Hymenoptera in their attacks on their prey, I was impressed with the jealous surveillance of the ants, and the protracted manœuvres of the hunters in deceiving these guardians. *Cemonus unicolor* Fabr. and *Pemphredon insigne* V. d. L., which I was especially able to follow, showed by their detours and subterfuges that their real enemy is not the aphid, but the ant which protects it." After quoting this passage Wheeler (1910, p. 353) goes on to remark that "Indeed, the fierce watchfulness of *Formica sanguinea* or *F. rufa* must be apparent to any observer who disturbs these ants while they are attending their aphids. The former at once open their mandibles and rush at the intruder and the latter throw back their heads, sit up with the tips of their gasters directed forward and discharge volleys of formic acid in the direction whence they are threatened. Belt has observed the workers of Pheidole protecting their membracids in a similar manner".

More recently Eidmann (1927) has studied in Germany the ant *Lasius niger* and its aphides. He regards it as definitely proved that "an energetic protection is afforded to the plant-lice colonies by the tending ants", which set a single sentry or a whole aphid-guard over the herds. These sentries do not milk the cows themselves, but protect them from enemies and parasites, and spread the alarm, if necessary, to the other ants. Strange ants were seized and bitten to death. A marked

* Un Hymenoptère ravisseur de Fourmis, *Act. Soc. Linn. Bordeaux*, 44: pp. 341–6.

sentry was observed at its post day after day for eight days, sometimes from early morning till late evening (Escherich, 1928). It seemed also that, in some cases at least, each aphis had its own special bodyguard, which returned to it every day. During the summer the other workers of the colony came to do most of their milking at night. These results must appear to the uninitiated almost a fairy tale, but the facts are vouched for by two sober and highly experienced observers.

For a long time Eidmann (1927) studied the aphis parasite, *Trioxys*, and was convinced that the ants " know how to guard their milch cows energetically against the attacks of the parasite ". The *Trioxys* " could oviposit in its victims only where the latter were not guarded by ants, which are certainly the chief factor in preventing the annihilating activity of these parasitic wasps becoming as efficient as one would expect. The protection is, however, directed, above all, against competition—that is against strange ants ". Eidmann goes on to describe combats he has witnessed between the herding ants and strangers, and concludes " The protective function of the aphid-guards is thus established beyond question ; nevertheless, their work seems not yet settled ".

Kirkpatrick, investigating the coffee mealy-bug (*Pseudococcus lilacinus*) in Kenya Colony, found that these insects multiply three times as rapidly when attended by ants—chiefly of the species *Pheidole punctulata*. He writes * : " The ant attends the mealy-bug for the sake of its sweet secretion or ' honey-dew ', at times it will also eat a little of the wax with which the mealy-bug is covered.

" In doing so it undoubtedly stimulates the mealy-bug to more rapid reproduction—whether the number of eggs laid is actually increased or whether, as is more likely, the mortality among the growing mealy-bugs is reduced, is not definitely known.

" Experiments with potted coffee plants have shown that although the mealy-bug is able to increase slowly in the absence of this species of ant, it will multiply at least three times as fast when they are in attendance. Mealy-bugs attended by ants appear much more vigorous and in better

* 1927. The common coffee mealy-bug (*Pseudococcus lilacinus*, Ckll.) in Kenya Colony [*Bull. Dept. Agric.*] Kenya, No. 18, 110 pp., 15 figs.

condition than those which are unattended—the fact that the ants remove dead mealy-bugs and cast skins doubtless contributes to this impression.

"However the real danger in the presence of *Pheidole punctulata* lies not so much in their direct stimulation of the mealy-bug, as in the fact that they destroy, in one stage or another, large numbers of many—possibly all—the beneficial insects which are predaceous on the mealy-bug. It certainly seems that the ants recognize that the enemies of the mealy-bug deprive them of the source of their favourite food, and kill them in order to get rid of them, for though they undoubtedly use some of the soft-bodied larvæ for food, they will also kill adult lady-birds which they have never been observed to eat.

"However numerous the ants may be, they do not kill by any means all the lady-birds and other predators on a coffee tree, and they will often pass them by without showing any signs of hostility. It has been repeatedly observed that if lady-birds are liberated on to a tree infected with mealy-bug and attended by this species of ant, the ants immediately show a much greater animosity towards them than they had previously shown to any which may have been on the tree before. This fact, which on the face of it appears to reveal an almost human intelligence on the part of the ant, was especially noticeable in the case of *Cryptolæmus montrouzieri*, Muls., which was imported from South Africa by the Department of Agriculture, and bred in numbers in the Laboratory. When they were released on to a coffee plantation, few survived the ants for more than three days.

"The larvæ of several of the indigenous predaceous lady-birds, as also those of *Cryptolæmus*, have a more or less close resemblance to mealy-bugs, which one would naturally suppose would afford them some measure of protection from the ants. On the other hand, the larvæ of the Lace-wing flies (Chrysopidæ) which camouflage themselves with the dead bodies of the mealy-bugs they have eaten, do appear to be thereby protected, as the only occasions on which the ants have been seen attacking Chrysopid larvæ have been when these have had no mealy-bugs on their backs, presumably having recently moulted. The larvæ of the moth, *Eublemma costimacula*, Saalm., is another mealy-bug eater which lives in a case made out of the remains of its victims, and this species has never been observed to have been attacked by ants." (Op. cit., pp. 46–7.)

Kirkpatrick lists at least five species of ladybirds, a fly, a lacewing, and three Psocids, which are predaceous on the mealy-bug and are destroyed by the attending ants.

" In addition to actual destruction, there is no doubt that the ants interfere with the feeding and oviposition of the predators. A number of ants may often be seen chasing a lady-bird, even though they frequently do not catch it."

MacDougall * observed in the Canary Islands, the relations between a mealy-bug (*Pseudococcus comstocki*) and the Argentine ant (*Iridomyrmex humilis*). He states that " the Argentine ant does not injure the banana plant but lives in association with the scale-insect and patrols the bananas so that the *Pseudococcus* is kept free from predaceous and parasitic insects ".

Bequaert (1922, p. 337) writes with reference to ants and their cows in general : " It is obvious that the ants protect the plant bugs by driving away coccinellid beetles, ichneumon flies, and other enemies." He gives, however, no specific instances of such active protection.

Wellenstein † (p. 37), after studying the wood-ant, *Formica rufa,* which milks the aphid *Lachnus pichtæ,* writes : " The ants protect their ' milch-cows ' against any Coccinellids [ladybirds] in the vicinity, by the furious attacks which they make on the small beetles."

A number of careful observers in other parts of the world, while admitting that parasitization of aphides and scale-insects is much less when ants are in attendance, deny that the parasites are actually driven away by the latter.

In Java, Keuchenius (1914, 1915) and Van der Goot (1915, 1916) believed that the ant, *Plagiolepis longipes,* protects in no way whatever from its natural enemies, the coffee scale-insect (*Lecanium viride*), which it assiduously attends for honey-dew. Nevertheless, a series of long and very careful experiments showed the latter worker that the presence

* MacDougall, R. S., 1926, *Pseudococcus comstocki,* Kuw., as an enemy of the banana (*Musa cavendishii*), *Bull. Ent. Res.*, xvii : pp. 85–90, pls. 7–13.

† " Beitrage zur Biologie der roten Waldameise," *Zeits. angew. Entom.*, xiv : pp. 1–68, 21 Abb., 1928.

of the ants exerts an extraordinarily favourable influence on the development of the scale-insect. On ant-infested bushes the death-rate of the scales is considerably lower; they develop more rapidly; their parasitization by Hymenoptera is reduced; and their progeny is actually twenty times more numerous. While denying any direct defence whatever against natural enemies, Van der Goot attributes this favourable result to promotion of more frequent excretion—for honey-dew is nothing but the sugar-rich excrement of these Homoptera—and to consequent acceleration of feeding and metabolism in general, by the constant "milking" on the part of the ants. The experiments of Bos on bean aphides in Europe, as described by Forel (1928, i, pp. 494, 497), seem to lead to a similar conclusion—on the lines of altered metabolism—though Forel believes the aphides are also directly protected, at least by the carton shelters which are built over them in this case.

There is obviously need for more extensive experiments and observations to ascertain in just what the favourable influence of the ants on their "cows" consists.

Note 14.—The whole question of "ants in their diverse relations to the plant world" has been reviewed in an extremely thoroughgoing manner, under this title, by Bequaert (1922). His great work, and that which follows it by Bailey, on the anatomy of ant-plants or myrmecophytes, must be consulted by all interested in this striking series of parasitic and symbiotic phenomena. It forms the basis of the present brief discussion (see also Notes 22–25 inclusive) of some of the questions raised by Lubbock.

Lubbock's observations on seed-carrying by some of the common European ants are among the first of a mass of data which are now leading naturalists to recognize the importance of ants in the distribution of seeds. Sernander (1906) has been the foremost student of these *myrmecochores*, or plants whose seeds are gathered by ants and incidentally or accidentally, but in any case extensively, dispersed by them. "His conclusions show that in Europe a great many grasses and herbaceous plants rely almost exclusively, or at least to a large extent, on certain species of ants for the successful scattering of their seeds. Many of the more common ants, belonging to such ubiquitous genera as *Formica, Lasius,* *Tetramorium*, and *Myrmica*, gather seeds of various plants more or less consistently. To the phytecologist these widely distributed ants are perhaps factors of greater importance than the true harvesters. The latter, to be sure, are more spectacular in their performances, but they are restricted to certain desert or semi-arid regions and are evidently extreme cases, remarkable for the huge quantities of seeds stored in their granaries.

" The ecological significance of seed-transporting ants can only be adequately realized upon closer scrutiny of the actual results of their activity in this line. Sernander's calculations, though based on moderate figures, show that the amount of seeds carried about by ants must be considerable. He found, for instance, that a single colony of *Formica rufa* transports during one season about 37,000 seeds and fruits. Observation also discloses that the seeds are in this way conveyed appreciable distances (100 to 200 feet) from the mother-plant. On their foraging excursions ants frequently drop or lose seeds along the road. Furthermore, many of the seeds finally stored in the recesses of the nest are sooner or later cast out near the entrance along with chaff and other débris from the ants' household, and a number of them are still able to germinate." (Bequaert, 1922, p. 356.)

NOTE 15.—The little Phorid fly, *Platyphora lubbocki*, discovered by Lubbock, and described by Verrall in the Appendix (p. 396) of the seventeenth edition (and also in earlier editions) of this work, has been proved by Donisthorpe to be the male of the still more puzzling wingless fly, *Ænigmatias blattoides*, found by Meinert in Denmark in 1890. The valid name for the species is thus *Platyphora lubbocki*. For an account of its habits and hosts, Donisthorpe (1927, pp. 129, 130) should be consulted.

NOTE 16.—In what Wheeler calls " the present colourless and noncommittal stage of natural history ", the study of insect temperament is sadly neglected. The entomologist who describes the behaviour of insects is usually haunted by one great fear—that of falling into the " eighth deadly sin " of anthropomorphism. Yet, as Whitehead has remarked, " if we wish to throw light upon the facts relating to organisms, we must study either the individual molecules and electrons, or the individual living beings. In between we find comparative confusion. . . . The characteristic laws of inorganic matter are mainly the statistical averages resulting from confused aggregates." And it is on just such "statistical averages" which "blur and obliterate the individual characters of the individual organisms" * that the tropic theory of insect behaviour is based. The progress not only of insect psychology but also of economic entomology will depend upon the increasing study of insects as organisms, and not as merely complicated mechanisms.

Schjelderup-Ebbe † notices that at least three of the types of human temperament, namely the phlegmatic, the sanguine and the choleric recur among the insects. The phlegmatic temperament is frequent among beetles, and in the caterpillars of butterflies and moths. It may be lost in the adult. Phlegmatic insects are slow-moving and often helpless.

The choleric temperament is exhibited by all Carabid beetles and Staphylinids, even the very smallest, and by the larvæ of dragonflies among others. The movements of choleric insects are generally very sudden and very lively, and the habits predatory. Many are armed with powerful jaws or stings.

The sanguine temperament is very frequent among all moths and butterflies; leafhoppers, bugs, Neuroptera, very many flies, some beetles and several Orthoptera. Extreme representatives of this type are blue-bottle flies and cockroaches.

Bees, according to Schjelderup-Ebbe, are at once both choleric and sanguine.

Phlegmatic types are even rarer among mammals than among insects; and no examples at all are known in birds.

A basis for the investigation of insect physiognomy has been laid in an illuminating paper by Wheeler,‡ who follows Kretschmer (1922) in recognizing two outstanding human types—the "asthenic" and the "pycnic"—and distinguishes analogues among the insects. The asthenic is pale, scrawny, long-limbed, with a "hachet face", reduced pilosity on body,

* A. N. Whitehead, 1928. *Science and the Modern World.* Lowell Lectures, 1925, pp. 139.

† 1924, Biologische Eigentümlichkeiten bei Insekten, *Ent. Zeits.*, Frankfurt-a-M., 38: pp. 41–2.

‡ 1927. The physiognomy of insects. *Quart. Rev. Biol.* 2, No. 1: pp. 1–36, 42 figs.

but often abundant on cranium. Mentally he is active, intense, introverted and dogmatic. The pycnic is rubicund, rotund, large bodied, short-limbed, moderately pilose, fond of eating and drinking, extroverted, easy-going and tolerant. In all the principal orders of insects there are whole genera or even families which conform to one or the other of these two types. But the vast majority of insects are intermediate "and if", says Wheeler, "I designate this group as 'athletic', the economic entomologists, who spend their lives ardently and often unsuccessfully wrestling with them, will certainly not object."

Insect physiognomy is determined very largely by the musculature. The limited and mechanical expression of the emotions in insects, Wheeler thinks, is due to the relative position of the muscles and the skeleton—a hard exoskeleton.

Examples are analysed, mainly from ants, and the whole paper, which teems with stimulating suggestions, should be consulted in the original.

NOTE 17.—Forel (1928, i, p. 469) describes again his own observations quoted by Lubbock, and adds that the cause of such activities "to-day . . . might, perhaps, be described by Freud as 'sublimated love'." After showing that both Stumper and Stäger have, within recent years, seen similar games among workers of the parasitic ant, *Formicoxenus nitidulus*, in the Alps, he concludes : "It is a well-established fact, therefore, that on fine, calm days when they are feeling no hunger or any other cause for anxiety, certain ants entertain themselves with sham fights, without doing each other any harm ; but these games come to an end directly they are scared. This is one of their most amusing habits."

NOTE 18.—The significance of ants licking one another and their larvæ is, in Wheeler's theory of trophallaxis (see Note 5) tremendously enhanced. The penchant of ants for licking exudates and secretions is exploited in the nests themselves by a vast horde of guests (see Note 31)—other insects which often bear tufts or patches of golden hairs or trichomes marking secretory areas ; and outside the nest is the basis of the dairy industry which forms such a noteworthy feature in ant activity. The craving for the secretions of the true guests or symphiles—in quantity infinitesimal, but in quality obviously highly excitatory—has been compared with alcoholism among men, and has been known to lead to similarly degenerative social results. Thus the Staphylinid beetles of the genera *Lomechusa, Xenodusa,* and *Atemeles,* and their larvæ are more carefully tended by their ant-hosts than is the ant-brood, on which, moreover, these beetle-larvæ are predatory. "In consequence of this infatuation the Lomechusa larvæ often destroy the greater part of the brood, so that in *sanguinea* colonies heavily infested with the parasites the queen larvæ develop abnormally. Either they are neglected or the ants actually endeavour to convert them into workers, because they feel that this caste is inadequately represented in the colony. But whatever be the treatment of such queen larvæ they develop into pathological adults, known as "pseudogynes" (Fig. 51*b*), abortive creatures, resembling workers in size and in the shape of the head and gaster, but with a more voluminous and convex thorax, approaching that of the queen. They are paler than the normal workers and very lazy, cowardly, and incompetent. Usually they constitute 5 to 7 per cent, less frequently 20 per cent or more of the personnel of an infested *sanguinea* colony. Their appearance in a nest indicates that the colony is in a diseased condition and on the road to extinction." (Wheeler, 1928, p. 207.)

It is, however, important to note that Donisthorpe entirely agrees neither with the above account of the origin of *pseudogynes* nor with that of their behaviour. He writes (1927, p. 39): "The *pseudogyne* is a wingless deformed-looking individual, combining the thoracic characters of the female, with the size and gaster of the worker. The characters of these forms vary greatly, no two specimens out of a considerable number being exactly alike. The colour is often much lighter than in the normal female; the number of the ovarioles is much reduced, being sometimes less even than in the normal worker; and macro- and micro-pseudogynes occur.

"They have been said to be useless and cowardly ants, but I have found that they will work, bite, spray acid, clean each other, and tend the brood, as do normal workers.

"Wasmann considers that they have been brought about—in *Formica* colonies—by the presence of beetles of the genera *Lomechusa* and *Atemeles,* and Wheeler has suggested that they arise from starved female larvæ. From my own experience with pseudogynes I do not consider that either of these hypotheses will always, or alone, account for their presence in a colony; as though both these stimuli may produce this state of things under certain circumstances, under others, some other cause, about which we know nothing at present, may produce the same result."

One of the most extraordinary cases in insect biology is that of a Javanese Reduviid bug (*Ptilocerus ochraceus*), which not only possesses trichomes with an exudation extremely attractive to one of the common East Indian ants, but employs these as an effective trap. The trichomes are on the venter, and become visible when the bug, on the approach of a suitable ant, raises its body in an inviting position. "The ant at once proceeds to lick the trichome, pulling all the while with its mandibles at the tuft of hairs, as if milking the creature, and by this manipulation the body of the bug is continually moved up and down" (Jacobson).* After some minutes the exudation begins to exert a paralysing effect on the still eagerly-licking ant, which begins to draw its legs and topple over. Then the bug, seizing it with its front legs, pierces and sucks it dry.

Note 19.—The majority of ants found new colonies in much the same way as wasps and humble-bees—that is to say, the fertilized queen descends from her marriage-flight, breaks off her wings and seeks a suitable shelter under stone or bark, where she remains for a varying period of weeks or months while her ovaries ripen and the bulky wing-muscles of her thorax are broken down and dissolved in the blood, which applies their substance to the building up of the eggs. The young larvæ from the latter are her first workers, which will enlarge the nest, forage for food, and rear the next brood.

This is Wheeler's *independent* method of colony formation. The other ways are variants of his *dependent* method, and may be studied first in the famous "blood-red slave maker", *Formica sanguinea.* The slave-making habit had been known since the time of Huber, but its origin, and the mode of colony formation in this species, remained alike unknown till a

* Jacobson, E., 1911. "Biological Notes on the Hemipteron *Ptilocerus ochraceus*." *Tijdschr. v. Ent.*, liv: pp. 175–9. More recently China has published a well-illustrated popular account based on Jacobson's original observations, and a re-examination of the insects: China, W.E., 1928. A remarkable bug which lures ants to their destruction, *Natural History Magazine*, i: pp. 209–13, 2 figs.

discovery of Wheeler in 1904 cleared up both problems. The *sanguinea* queen is quite unable to found a colony by herself. She may therefore " adopt one of three courses : she may return to the nest in which she was reared or enter some other *sanguinea* nest, or she may invade a nest of *F. fusca*. As the first and second courses are sometimes adopted by other ants and do not lead to the formation of mixed colonies, they need no further consideration in this place, and we may confine our consideration to the last. As soon as the *sanguinea* queen invades a *fusca* colony, she becomes greatly excited and interested in the brood, seizes and collects in a small pile as many pupæ as she can snatch up and mounts guard over them. She slays any *fusca* workers that are bold enough to attempt to regain their property and is therefore soon left in undisputed possession of her plunder. Eventually *fusca* workers emerge from the cocoons and at once assume a friendly attitude towards the queen, feed her by regurgitation and behave towards her as if she were their own mother. She begins to lay eggs and the resulting larvæ are fed and reared by the black workers, so that when the *sanguinea* emerge a mixed colony is established. These workers show that they have inherited their mother's proclivities by kidnapping a brood of neighbouring *fusca* colonies, but they do this as an army and carry the *fusca* brood to their nest. In some colonies, as I have stated, this kidnapping, or slave-making proclivity may disappear after a time, and in *aserva* it seems to disappear very early or perhaps is not even inherited by the workers. In such cases, therefore, the personnel of old colonies may be made up entirely of *sanguinea* after the batch of *fusca* workers kidnapped and reared by the queen has died of old age. It is evident that slavery is at bottom a form of predatism and has its origin in the inability of the young queen to establish a colony without the aid of workers." (Wheeler, 1923, pp. 209, 210.)

The queen ants of the genus *Polyergus* or " amazons ", are likewise unable to found new colonies independently. Emery found that the young *Polyergus* queen enters a small and weak colony of *Formica fusca*, kills its queen by piercing her head, and is thereafter adopted by the *fusca* workers, who rear her brood, the members of which will later engage in slave raids on other *fusca* nests.

Queens of certain *Formica* and other species in various parts of the world secure adoption in the nests of totally unrelated ants, whose queen is made away with, sometimes by direct slaughter and sometimes by means not yet elucidated. The brood of the invader, which Wheeler distinguishes as a *temporary social parasite,* is reared by the host workers, which themselves in time die out, leaving a pure colony of the parasite species, " without showing any signs of its parasitic origin."

For more detailed information on colony formation, with further variants of the two main methods outlined above, the reader should consult the larger works of Wheeler, Donisthorpe, and Forel.

NOTE 20.—Since Lubbock wrote, the habit of instituting these living storehouses has been proved much more widespread than he supposed. " The condition here described, or one of less gastric distention, has been observed in desert or xerothermal ants in very widely separated regions and belonging to some nine different genera of Myrmicinæ, Formicinæ, and Dolichoderinæ (Myrmecocystus and Prenolepis in the United States and Northern Mexico, Melophorus, Camponotus, Leptomyrmex and Oligomyrmex in Australia, Plagiolepis and Aëromyrma in Africa and Pheidole in Australia and the south-western United States) ". (Wheeler, 1923, p. 180.)

The supposition of Lubbock that the habit had arisen independently in the two honey-ant genera known to him, is thus abundantly corroborated. Honey-ants have probably been evolved again and again in response to the favouring desert or semi-arid conditions described by Wheeler.

NOTE 21.—The relations between flowers and insects interested Lubbock so much that he devoted to them a whole book.* The literature on the subject, both erudite and popular, has now reached colossal proportions. The phenomena of " flower-biology " with those of " mimicry " probably constitute the strongest evidence for the natural selection theory of organic evolution. It is as useless to deny the existence of the remarkable adaptations between flowers and their insect visitors as it is to ignore the often extraordinarily close

* " On British wild flowers considered in relation to insects," *Nature Series*, 1875.

resemblance between animals and portions of their animate or inanimate environment—or to attribute either set of phenomena to chance. While admitting the facts, however, we are by no means compelled to accept the natural selectionist's explanation, because it is the only one in the field.

Lutz,* who is extremely anti-selectionist and very negativistic in his views on the problem, complains that the natural selection theory of insects and flowers "was propounded and has continued to be discussed on the basis of the colours as man sees them and with the assumption that the vision of insects is like that of man. Not only are floral colours not what they seem to us to be, but the vision of insects is quite different from normal human vision" (p. 233).

As a result of his experiments and observations Lutz comes to the following conclusions (pp. 277–8) :—

"Plants in their ordinary physiological processes produce coloured substances. These coloured substances are not confined to the inflorescence. Under certain conditions the green chlorophyll either disintegrates or is not formed and in its absence the colours of other substances are more apparent" (p. 277).

"Certain insects, such as bees, visit flowers in order to get food for themselves or their larvæ. In making these visits they frequently effect a transfer of pollen from one flower to another, and this transfer seems in some (but by no means in all or even in most) cases to be distinctly beneficial to the plant.

"The flower-visiting insects belong to a class of animals that is noted for well-developed olfactory powers and poorly developed vision. The females of a large order of insects (Lepidoptera) select special leaves upon which to lay their eggs, and this selection is probably made on the basis of odour, almost certainly not by sight. Flower-visiting insects come in large numbers to many visually inconspicuous flowers and are practically absent from many conspicuous ones.

"All of the colours of the spectrum from red to ultra-violet, both included, are to be found in light reflected by

* Lutz, F. E., 1924. Apparently non-selective characters and combinations of characters, including a study of ultra-violet in relation to the flower-visiting habits of insects. *Ann. Acad. Sci. New York*, 29: pp. 183–283, 7 pls., 48 figs.

one flower or another. Of these waves of light reflected by flowers, those of relatively great length, red to green, are more common than those of shorter length, blue to ultraviolet. Flower-visiting insects do not see red to green as well as they do blue to ultraviolet.

" In view of these fairly well established points and of others less well established, it seems to me reasonable to conclude that floral colours have developed simply as byproducts of the plant's metabolism ; that at most they are of only incidental and minor service to insects in finding flowers, and that they have not been developed by any action of natural selection. It would be rash to hazard an opinion as to whether nectar-secreting, odoriferous hypertrophies (flowers) would have been developed in connection with the sex-cells of plants apart from the visits of insects ; but it seems safe to say that, had such hypertrophies developed from any cause whatsoever, they would be coloured solely because of the physiological processes of the plant and not because the particular colours are of any more value to the plant than the colours of the purely physiological galls on its leaves " (p. 278).

It seems to us incontrovertible that, although we are utterly ignorant as to how they have arisen, the colours, forms, and odours of flowers are utilized to a very great extent by insect visitors as guides in the discovery and recognition of definite plant species. The criticism by Lutz and other extreme anti-selectionists in so far as it is directed against proofs of the utilization, rather than the origin, of floral characters, is really based on a Loebian misconception of insect behaviour, and its dependence on simple single stimuli evoking " forced movements ". Obviously utilization and recognition of signs are inconceivable as elements in such behaviour. It is now generally admitted that the facts of distant orientation, in insects as in other animals, are readily explicable by the hypothesis of the utilization and recognition of an *ensemble* of sensory cues, without the aid of any magnetic, electrical or any other mysterious " senses " whatever. Why not credit the anthophilous insects with a similar capacity in their search for nectar ?

Note 22.—" The so-called bull's horn acacias of Mexico, Central America, and Cuba are apparently true myrmecophytes; their stipular thorns are much enlarged and flattened or inflated; they are usually hollowed out by ants, which pierce an entrance below the tip of the thorn, more rarely near its base, and establish their nests inside; furthermore, the young leaves bear at the tips of their pinnæ minute, bright yellow food-bodies (Beltian bodies) * which are eagerly collected by the ants and carried inside the thorns. These plants all grow in dry or semi-desert regions under conditions very different from those of other myrmecophytes." (Bequaert, 1922, p. 510.) Certain somewhat similar acacias in Africa are found with swollen thorns, sometimes inhabited by ants, but there is a good deal of evidence that the swellings in this case are galls caused by other insects, and that the plants are in no sense true myrmecophytes. (Bequaert, loc. cit., p. 373.)

That ants receive considerable benefit from their close association with bull's horn acacias and other plants, is obvious, but that the plant gets much advantage from the partnership is by no means proved. Wheeler's summing up (1910, pp. 294, 308, 314) is still apposite, and I am aware of no observations which have since materially modified his conclusions. He writes: "The hypothesis of intimate mutualistic relations between ants and the higher plants is one of those fascinating constructions in which certain gifted and imaginative botanists have rivalled the inventors of the mimicry hypothesis in the zoological field. Both of these constructions have been treated as facts of the utmost value in supporting a still more general hypothesis—that of natural selection, and both, after having been carried to extremes by their respective adherents, are now facing the reaction that is overtaking Neodarwinism. Authors like Fritz Müller, Schimper, Huth, Delpino, Beccari, and Heim have marshalled a formidable array of observations in favour of the view that many plants develop elaborate structures to be used as lodgings

* "Meneghini and Savi (1844), Fr. Darwin (1877), and A. F. W. Schimper (1888), who have studied the inner structure and development of these Beltian bodies, all agree that they are homologues of the glandular serrations which frequently occur on the margins of young leaves. Such glands often secrete mucus or resin and, as a rule, disappear at an early stage; while in the ant acacias they increase considerably, are filled with proteins and fats and, when not removed by the ants, finally drop off." (Bequaert.)

by certain pugnacious ants or even furnish these insects with exquisite food substances, and in return for these services are protected by their tenants from the leaf-cutting ants or from other leaf-destroying animals. These observations are now being subjected to critical revision by authors like Rettig and H. von Ihering, whose attitude towards the whole subject is avowedly sceptical and reactionary."

Wheeler then proceeds to review a number of the cases which have been brought forward. Here we may instance one of the best known, that of the imbauba (*Cecropia*) of South America, whose hollow stems are tenanted by ants of the genus *Azteca*. "Those who have seen the living imbauba and its occupants are unanimous in describing the insects as rushing out and fiercely attacking any one who ventures to touch the foliage. Alien ants, especially, are vigorously assailed, and either killed or driven from the tree. Von Ihering, however, calls attention to the fact that various Chrysomelid larvæ, caterpillars, and the sloth (*Bradypus tridactylus*) are permitted to feed on the leaves unmolested. Fritz Müller and Schimper believed that the *Azteca* protects the tree from defoliation by the large leaf-cutting ants of the genus *Atta*, but von Ihering has shown that the plant, even when entirely free from its so-called protectors, is rarely or never visited by *Atta*. It thus appears that the *Cecropia* is not known to have any enemies against which the *Azteca* could avail. The animosity of these ants is probably greatest against alien colonies of their own species, and is directed to obtaining possession of the feeding grounds and neighbourhood of their nest. This is, of course, a well-known trait of ant-colonies in general. Although von Ihering says that 'in order to thrive the imbauba no more requires the *Azteca* than a dog does fleas', he nevertheless believes that the Müllerian bodies and the prostome * are myrmecophilous adaptations. In this, he seems to me to concede too much, for if the ants are of no use to the *Cecropia*, why should the latter develop structures for the purpose of attracting and retaining this superfluous bodyguard? And of the three Cecropian structures, which might be regarded as indicating

* The prostome is a depression near the top of an internode in *Cecropia* where the walls lack fibro-vascular bundles, and are most easily perforated by the colonizing queen ant.

myrmecophily, namely, the cavities of the trunk and branches, the prostomes and the Müllerian bodies, the first can hardly be an adaptation to harbouring ants, the second are produced, or at any rate, started, as Schimper admits, by the pressure of the axillary buds against the surface of the internodes, while the Müllerian bodies, though continually formed anew as they drop off or are carried away by the ants, may have an excretory or some other nonmyrmecophilous function, for aught that is known to the contrary. The adaptation, therefore, has every appearance of being on the side of the ant rather than on that of the tree."

At the close of his review of the question Wheeler remarks, "No doubt the various cases cited in the preceding pages are of great interest, both to the botanist and myrmecologist, but it is equally certain that none of them has been studied with sufficient care to warrant the conclusions advocated by Belt, Schimper and others. The relationships under discussion are all compatible with the view that the ants have adapted themselves to the plants—*plantas itaque norunt formicæ*—but the converse of this proposition is in most, if not in all instances, open to doubt. Travellers and naturalists who observe for a short time in the tropics, where all of these wonderful cases occur, are very apt to jump to conclusions, and carefully devised experiments, which alone can throw the necessary light on the subject, are still wanting."

Wheeler's own later observations * served only to confirm his doubts as to any benefits derived from the association by the plants.

Note 23 (see also Note 14).—The following is Lubbock's own note (pp. 416–18 of Appendix G) in the seventeenth edition) on this passage :—

Ants and Seeds of *Melampyrum pratense*.

M. Lündstrom has recently called attention to the interesting fact that the seeds of this plant closely resemble pupæ of ants in size, shape, and colour, even to the black mark at one end. He has suggested, very ingeniously, that this may be an advantage to the plant by deceiving the ants, and thus inducing them to carry off and so disseminate the seeds.

* "Observations on the Central American Acacia ants," *Trans. 2nd Ent. Congr.*, Oxford (1912), pp. 109–139, 1913.

There seemed, however, some improbability in the idea that ants should be deceived as to their own sisters. M. Lündstrom has found seeds of this species in ants' nests, but has not actually seen ants carrying them off, and I thought it would be worth while to determine this.

Accordingly I took ten seeds and placed them just outside one of my domesticated nests of *Lasius niger*. A certain number of ants were outside, and I saw several come up to the seeds, but they took no notice of them. I left them lying there for two days. I then tried them with another nest, the roof of which consisted of two plates of glass, side by side, but with an interval between them. I placed the seeds in this interval, and uncovered one of the sides. The ants immediately began carrying the pupæ which were thus exposed to the light to the other (covered) part of the nest, in doing which they necessarily passed close to the seeds, but they did not take the slightest notice of them. This operation was finished at 11 a.m., and I left them undisturbed till 12, the seeds remaining unnoticed and untouched. I then moved the cover from one half of the nest to the other, and the ants immediately began transporting the pupæ to the shaded half. One or two of them examined the seeds, not one of which, however, was moved. This took about an hour. At 4 p.m., however, three of the seeds had been carried in, and the next day at 7 a.m., two more seeds had been carried in. I then removed them, and put them just outside one of my nests of *F. fusca*.

31st August. 7 a.m. None have been touched. I now put the covering close to, but not over them. The ants took no notice of them.

2nd September. I now placed them just in the entrance of the nest, and covered over a part just outside: the ants collected as usual under the cover. I then removed the cover just inside the nest, so that the ants to reach it had to pass among the seeds. They, however, came in, but did not move a single seed. I once again moved the cover outside, and they followed it as before, but without moving the seeds.

So far as these observations go, it would seem that *F. fusca* takes no notice of these seeds, but that they really are under certain circumstances carried off by *Lasius niger*.

Note 24.—Is the stored grain generally prevented from germinating? This question has since been studied experimentally by Emery and other workers, in *Messor barbarus*, and the results summarized by Bequaert (1922, p. 362), who writes " When a ripe, dry, and unsprouted grain of wheat is offered to this species, the ants carry it into their nest and sooner or later gnaw off the embryo, always beginning to eat the grain at that end. This was even known to the ancient writers (Plutarch and others) who consequently attributed to the harvester ants a most wonderful instinct of preventing the sprouting of the grain by removing the germ. Emery, however, has shown experimentally that this is due merely to a matter of taste or gluttony manifested by the ants for this daintiest part of the grain. He believes that the ants mutilate the radicle of sprouted seeds for a similar reason, though he admits that this behaviour may be of a more complicated nature.

" Harvester ants can thrive perfectly on unsprouted grain, as shown by Emery's experiments, but in most cases they allow a partial germination of the seeds before using them as food. . . . It has been supposed (Moggridge) that the ants allow the seeds to germinate in their nests so the starch will be converted into grape sugar, the whole procedure being somewhat comparable to the malting of grain. Neger, however, discards this explanation because he found that in the sprouted seeds which are placed to dry in the sun the process of germination was not sufficiently advanced to convert any large quantity of starch. He believes, therefore, that the practice of allowing them to sprout has no further purpose than to facilitate the removal of the coatings, which are sometimes very hard to detach from ripe seeds; on sprouted seeds, these envelopes split open and are then easily peeled off by the ants."

NOTE 25.—Do ants actually cultivate seed plants? This question is still *sub judice*. Since ants and termites are well known deliberately to cultivate, and start new cultures of, various specific fungi, there can be no *a priori* negative.

With regard to the harvesting ants, Wheeler writes (1910, p. 286): " The Texan harvester has attracted no little attention on account of Lincecum's statement that it actually sows the seeds of the ' ant-rice ' (*Aristida stricta* and *oligantha*) around the periphery of its disks or mounds, and cultivates the crop in addition to harvesting and storing it in its granaries.

This notion, which even the Texan schoolboy has come to regard as a joke, has been widely cited, largely because Darwin stood sponsor for its publication in the *Journal* of the Linnean Society. McCook, after spending a few weeks in Texas observing *P. molefaciens* and recording his observations in a book of 310 pages (1879c.), failed to obtain any evidence either for or against the Lincecum myth. He merely succeeded in extending its vogue by admitting its plausibility. Four years of nearly continuous observations of *molefaciens* and its nests enable me to suggest the probable source of Lincecum's misconception. If the nests of this ant can be studied during the cold winter months—and this is the only time to study them leisurely, as the cold subdues the fiery stings of their inhabitants—the seeds, which the ants have garnered in many of their chambers, will often be found to have sprouted. Sometimes, in fact, the chambers, are literally stuffed with dense wads of seedling grasses and other plants. On sunny days the ants may often be seen removing these seeds when they have sprouted too far to be fit for food, and carrying them to the refuse heap, which is always at the periphery of the crater or cleared earthen disk. Here the seeds, thus rejected as inedible, often take root and in the spring form an arc or a complete circle of growing plants around the nest. Since the *Pogonomyrmex* feeds largely, though by no means exclusively, on grass seeds, and since, moreover, the seeds of *Aristida* are a very common and favourite article of food, it is easy to see why this grass should predominate in the circle. In reality, however, only a small percentage of the nests, and only those situated in grassy localities, present such circles. Now to state that the *molefaciens*, like a provident farmer, sows this cereal and guards and weeds it for the sake of garnering its grain, is as absurd as to say that the family cook is planting and maintaining an orchard when some of the peach stones, which she has carelessly thrown into the backyard with the other kitchen refuse, chance to grow into peach trees.

"There are several other facts that go to show that the circle of grass about the *molefaciens* nests is an unintentional and inconstant by-product of the activities of the ant-colony. First, the *Aristida* often grows in flourishing patches far from the nests of *molefaciens*. Second, one often finds very flourishing ant colonies that have existed for years in the midst of much travelled roads or in stone side-walks thirty meters or more from any vegetation whatsoever. In these cases the ants simply resort for their supply of seeds to the nearest field or lawn, or pilfer the oat-bin of the nearest stable. Third, it is evident that even a complete circle of grass like that described by Lincecum and McCook would be entirely inadequate to supply more than a very small fraction of the grain necessary for the support of a flourishing colony of these ants. Hence they are always obliged to make long trips into the surrounding vegetation, and thereby wear out regular paths which radiate from the cleared disk in different directions, often to a distance of 10–20 m. from the nest. These paths, in the case of the typical Mexican *barbatus* remind one of human footpaths, as they may be as much as 10–15 cm. wide. The existence of these well-beaten paths, which are often found in connection with grass-encircled nests, is alone sufficient to disprove Lincecum's statements."

There is another aspect to the present question. In 1902 Ule gave the name of " ant-gardens " to " certain sponge-like ant-nests which he found built on the branches of trees in the forests of the Amazon. These nests consist of soil carried up by the ants (*Azteca olithrix, ulei,* and *traili* and *Camponotus femoratus*) and held together by the roots of numerous epiphytes, which grow out of it on all sides, making it resemble the head of a Medusa. The ants not only perforate the soil with their galleries but, according to Ule, actually plant the epiphytes. This he infers from seeing the insects in the act of carrying the seeds". (Wheeler, 1910, p. 315.) These ant-gardens have since been studied in greater detail by Wheeler (1921) and by Bequaert, and it may be said at the outset, that the evidence for actual cultivation here, is very much greater than in the case of the Texan harvesters. Forel (1928, I, pp. 518–23) appears indeed to be convinced by Ule's exposition of the facts ; but he had apparently only seen specimens which had been sent to Europe. He writes (p. 521) : " I may add that as ants can neither build nor dig out durable nests in flooded country, ant-gardens replace all structures of this kind, except the carton nests built by certain species. Even on dead trees, ant-gardens continue to thrive for a long time, acquiring a purplish colour, whereas other isolated epiphytes, not cultivated by ants, are doomed to die quickly. In view of these facts I do not understand how Wheeler can still contend that 'it is quite as probable that the seeds are sown by the wind'."

Wheeler (1921), who has investigated the "ant-gardens" in British Guiana, disagrees in several important respects with Ule's interpretation. His remarks have been summarized by Bequaert (1922, p. 368) as follows: ". . . though the same plants do not occur in all gardens, no preference of certain ants for certain plants could be detected. All the species of ants found in the ant-garden biocoenose may also nest elsewhere, but it must be admitted that *Camponotus femoratus* shows a decided preference for the garden nest, so that we have here a very regular and intimate ethological relationship between an ant and certain epiphytes. According to Wheeler the ant-gardens are not started in the manner implied by Ule, viz. by means of the ants either putting seeds into crevices or accumulating a certain amount of humus at some spot on a tree or bush, and then collecting and planting the seeds in the mass. It is more probable that the young ant epiphytes originally grow in small accumulations of earth or detritus, which are ultimately settled by colonies of the ants. That the amount of humus is gradually increased by the ants with the growth of the colony admits of no doubt, and it is possible that as the accumulation becomes greater, it may be sown with seeds falling from the original plant. Furthermore, it is practically certain, from what we know of the habits of ants, that new gardens cannot be seeded from old ones, as Ule maintains, for this would be too great a task for the single fecundated queens which start the new colonies. Ule's experiments with ants transporting the seeds of these epiphytes do not furnish conclusive proof that the insects actually sow the plants, for ants will often carry all sorts of portable organic bodies into their nests, only to cast them out later when they find them useless. And lastly, Ule records no convincing observations in support of his contentions that the ants actually cultivate the growing plants. Wheeler believes, therefore, that it is advisable to suspend judgment for the time being as to the provenience and significance of the plant elements in the ant-garden biocoenose of tropical America."

Note 26.—The extraordinarily close resemblance of a host of entirely unrelated Arthropods to ants has attracted the attention of observers in every part of the world. There are spiders, beetles (even weevils), bugs, grasshoppers which at first sight can deceive even the forewarned entomologist time and time again. In a typical case the likeness in colour and form is very greatly strengthened by ant-like movements which often differ conspicuously from the behaviour of the insect's close but un-antlike relatives. Thus myrmecoid spiders habitually elevate the first pair of legs and wave them like an ant's antennæ.

This three-fold myrmecoidy occurs so often that any explanation relying on coincidence is put right out of court. If the resemblance is of any biological significance—and he who would deny this must either be unfamiliar with the best examples or unusually tough-minded—we can hope for light on its origin only through the closest study of the animal's relations with the environment. And unfortunately this analysis has in no case been pushed very far. Naturally enough, we should seek first an explanation in terms of the animal's relations, direct or indirect, with ants, and more particularly with the ants which it specifically resembles; for the problem is little concerned with a general likeness to ants, but more often with a highly specific resemblance to certain ants which abound in the animal's haunts. A general likeness to ants may be explained in ant-guests, as Wheeler has suggested, by the influence of a common environment—the very specialized conditions, humid, warm, dark, and crowded, of the nest. At least in certain cases, among animals which enter into no relations with ants, it has been attributed by Heikertinger * to the influence of cavern-life. But as Heikertinger himself points out, these cavernicolous types are essentially similar to some of the most myrmecoid of the ant-guest beetles, and neither the ones nor the others are really as ant-like as the latter are claimed to be, since they all lack the wide head so characteristic of ants. Their most ant-like features—the narrow waist and the enlarged and swollen abdomen—certainly seem, like these characters in the ants themselves, closely connected with a subterranean existence.

* Heikertinger, F., 1927, "Die Ameisenmimese. IV. Die Lösung des Problems, *Biol. Zentralbl.*, Bd. 47: pp. 462–501, 47 Abb.

In other cases, the ant-like animal is still not greatly divergent in form from its nearest relatives. Almost any moderately small, wingless Hymenopteron, with a wide head is necessarily considerably ant-like, notably certain Dryinids. Some Cicindelid beetles also approach ants in form without diverging greatly from their family type. Heikertinger has stressed these cases, which he explains, naturally enough, by the "Wachstumrichtungen" or growth-tendencies of the groups concerned.

So much for a general resemblance to ants. There remains, however, the gist of the problem—the ever-increasing cases of specific resemblance. Heikertinger would attribute these to "chance", a concept which in his later work (1927, p. 500) he defines as "genetic independence of protective function".* As to this hypothesis, we can take it or leave it. A much more popular theory is that of "mimicry" in terms of natural selection, which we must now examine.

Wasmann, the great student of ant-guests, and the chief opponent of Heikertinger's views, believes that true ant mimicry is found only in the resemblance of myrmecophiles to their hosts, and that "its function is to deceive the host-ant in order that the guest may either devour ants and brood or pursue in or near the nest more peaceable occupations undisturbed by the former". †

He distinguishes between "sight-mimicry" and "touch-mimicry", reserving some of his most enthusiastic encomiums for examples of the latter, in which the general form of the guest may be exceedingly un-ant-like, but certain contours and sculpturings resemble, it is said, parts of the body of the host-ant. Instances are illustrated among the guests of the blind or short-sighted driver-ants (Dorylinæ). The fundamental basis for this theory—namely, the proof that ants are deceived by these resemblances—is practically entirely lacking. The true guests or symphiles carry a passport to the ants' favour in their secretions, of which the hosts are so

* "wobei als 'Zufall' die genetische Beziehungslosigkeit zur Schutzfunktion zu verstehen ist."

† Myers and Salt, 1926. The phenomenon of myrmecoidy, with new examples from Cuba. *Trans. Ent. Soc. London*, 1926, pp. 427–36, pl. 93, 1 fig. To this paper the reader is referred for a discussion of the subject and citations of the literature, other than that in the bibliography at the end of this book.

inordinately fond; while the other myrmecophiles are protected apparently only by their agility or by their armour and "awkward" shape.

There is now considerable evidence, notably in a most interesting recent paper by Hingston (1928) * that ant-like spiders often prey upon the ants which they specifically resemble and in whose haunts they occur; but there is not the slightest indication that they are enabled to do so by deceiving the ants into mistaking them for fellow workers.

Most mimeticists believe that the chief advantage of ant-mimicry lies in the protection afforded from the attacks of predaceous animals—a theory which brings myrmecoidy into line with other forms of mimicry as explained by the natural selection hypothesis. On this theory, ant-like forms need live in no direct relationship with ants, but need only occur in the same general haunts as their "models", for which they may be mistaken by potential enemies. The necessary support for such a theory lies in a demonstration that ants are immune from the attacks of predaceous enemies to a sufficient extent to render such relative immunity worth sharing. Poulton and others have shown that predaceous Arthropods show very little discrimination in the choice of prey. This applies to relatively general feeders which are, of course, the only kind against which mimicry would conceivably act as a defence; for the activities of such specialized predators as many of the solitary wasps necessarily lie as far outside the range of the mimicry problem as do those of specific parasites. We therefore find considerable agreement that the devices of the mimetic insect are operative, if at all, against the attacks of vertebrate enemies.†

The direct evidence that ants are in any way protected

* Hingston, R. W. G., 1928. "Field Observations on Spider Mimics," *Proc. Zool. Soc. Lond.* (1927), pp. 841–58, figs. 1–10. In Hingston's paper we are introduced to a Thomisid spider (*Amyciœa* sp.), which is an exponent of back to front mimicry. It occasionally walks backwards, and bears spots on its abdomen which Pocock thinks mimic the eyes of an ant! Another spider (*Dipœna* sp.) mimics the heads of decapitated ants, thrown on the refuse-heap of the nest!

† Nevertheless, Hingston (l.c.) makes the statement that spiders are persistently preyed on, chiefly by Diptera and Hymenoptera, and that wasps, as Pocock also believed, are their greatest enemies, from which he assumes they obtain a large measure of protection by "mimicking" ants. It is necessary again to emphasize the entire absence of experimental evidence.

against insect-eaters seems to be almost lacking. On the other hand, data to show that these insects form a frequent and considerable part of the diet of many diverse vertebrates are steadily accumulating (see Note 27). In commenting on the exhaustive treatise by Bequaert on the predaceous enemies of ants, Poulton (1924) claims that the very fact that ants are dominant insects, common and conspicuous and "advertised by their communities as well as by their appearance . . . in itself supplied the evidence of special defence that Dr Bequaert apparently believed to be lacking". He believes also that the great variety of means by which ant-resemblance is brought about and the modification of colour, form, and behaviour, which contribute to the result, all compel us "to believe that there is something advantageous in the resemblance to an ant, and that natural selection has been at work. The phenomena do not merely disprove all other suggested causes of change, but they constitute the most powerful indirect proof of the operation of natural selection." (Poulton, l.c.) Such is the stoutest definition of the selectionist position and the strongest statement of the mimicry hypothesis,—the only theory which apart from the doctrine of "chance", explains the phenomena of myrmecoidy. Should we therefore accept it, unsupported as it is by direct evidence ? "Nous répondons,* tout simplement, que nous ne savons pas de quoi dépendent les transformations spécifiques des êtres vivants (si ces transformations spécifiques ont lieu) ; mais que nous préférons admettre notre ignorance totale que de nous attacher avec obstination à une idee qui est évidemment fausse et puérile, qui a fait naître et fait naître encore une infinité de spéculations d'une absurdité monumentale."

Note 27.—The parasitic enemies of ants include a number of very extraordinary animals.

Among the least harmful are the little Phorid flies of the genus *Metopina*, whose "small larva clings to the necks of the ant-larva by means of a sucker-like posterior end and encircles its host like a collar. Whenever the ant-larva is fed by the workers with pieces of insect placed on its

* Thompson, W. R., 1923, p. 200. "Recherches sur la biologie des Diptères parasites," *Bull. biol. France et Belg.*: T. 57, pp. 174–237. The passage quoted concerns the natural selection theory in general, but applies with even greater force to the mimicry hypothesis in particular.

PLATE IV

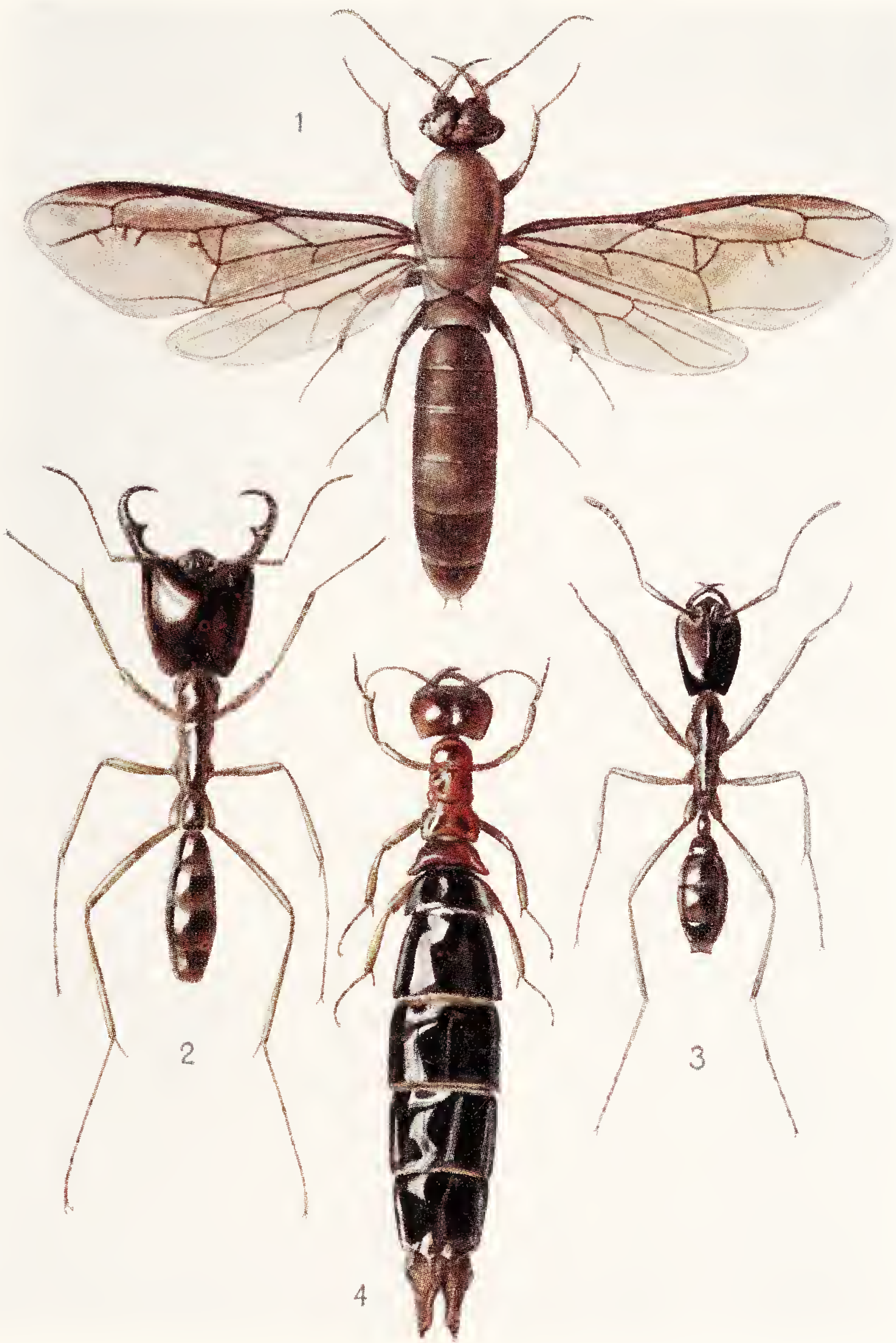


Fig. 1. *Dorylus nigricans*, male. An African driver ant ($\times 1\frac{1}{2}$)
,, 2. ,, ,, large worker ($\times 3$)
,, 3. ,, ,, small worker ($\times 4$)
,, 4. ,, ,, female ($\times 2$)

[*face p.* 288

trough-like ventral surface, within reach of its mouth-parts the larval *Metopina* uncoils its body and partakes of the feast; and when the ant-larva spins its cocoon it also encloses the *Metopina* larva within the silken web. The commensal, however, moves to the caudal end of its host and forms a small, flattened puparium which is applied to the wall of the cocoon. This is obviously an adaptation for preventing injury from the jaws of the worker ants when the cocoon is being opened, and the callow extracted from its anterior end. The ant hatches before the *Metopina* and the empty cocoon with the puparium concealed in its posterior pole is carried to the refuse heap. There the fly emerges and escapes from the cocoon by the opening through which its host emerged. The *Metopina* larva consumes so little food and is so considerate of its host, that it can hardly be said to produce any injurious effect on the colony; at any rate, the larvæ which have borne commensals develop into perfectly normal workers. The ants clean the commensals while they are cleaning their own progeny, and show no signs of even being aware of their presence in the nest". (Wheeler, 1920, p. 412.)

Several little hemispherical mites of the genus *Antennophorus* live as ectoparasites on the bodies of certain ants (*Lasius*) and are noted for their habit of orientating themselves symmetrically on the host. If there be two on an ant, they will cling one on each side of the head or of the gaster, quite balanced; if a third is present, it attaches itself to the throat, and so on. "When attached to the head the mite obtains its food by drinking from the regurgitated droplet as it is being passed to or from the mouthparts of the host, or it titillates the ant with its antenniform legs and induces her to regurgitate for its special benefit." (Wheeler.) "Perhaps we can best appreciate the relations of the ants to the mites, if we fancy ourselves blind, condemned to live in dark cellars and continually occupied with pasturing and milking fat, sluggish cows, yielding quantities of strained honey instead of milk. Then let us suppose that occasionally there alighted on our cheeks or backs small creatures which, by placing themselves in positions symmetrical to the median longitudinal axis of our bodies, took great care not to annoy us, and stretched forth to us from time to time small, soft hands, like those of our friends, begging for a little honey, should we not under the circumstances, treat these little Old Men of the Sea with much lenity and even with something akin to affection? " (Wheeler, 1923, p. 227.)

There is a number of brilliant metallic, grotesquely-spined Chalcidid wasps of the family Eucharidæ, whose larvæ live in the nests of ants (*Pheidole*, *Solenopsis*, *Camponotus* and others) and attach themselves to the necks of the ant-grubs, whose juices they suck, not to directly fatal extent, but sufficiently to cause weakening and failure to develop to the adult state. In *Orasema*, studied by Wheeler, both the parasite larva and the adult are licked by the ants, and the latter even fed. *Orasema* probably lays its eggs in the nest, but *Schizaspidia*, studied in Japan by Clausen,* and *Stilbula* investigated in France by Parker and Thompson,† lay enormous numbers of very minute eggs, in the buds of certain trees. The little *planidium* larva, which hatches from the *Schizaspidia* eggs next summer, is only about a tenth of a millimetre long. It manages to attach itself to the feet of ants which climb the tree in search of food, and is carried to the nest, where it eventually finds the ant-brood, settles on a larva, and sucks its juices after the manner of *Orasema*.

The internal parasites of ants include the Phorid fly, *Apocephalus*, which lays its eggs on the head of certain North American ants. The young larvæ enter the head cavity through the occipital foramen " and feed on the tissues, causing the ant to become very lethargic. Later the creature literally loses its head, and the larvæ pupate and hatch. Pergande has described the frantic efforts of the ants to rid themselves of these terrible executioners ". (Wheeler.)

Finally, larval threadworms of the genus *Mermis* " enter the larva [of several neotropical ants] and apparently by unduly stimulating its appetite cause it to be fed excessively, so that it becomes unduly large at the time of pupation and produces a gigantic worker form, with ocelli . . . which I have

* Clausen, C. P., 1923. The biology of *Schizaspidia tenuicornis*, Ashm., a Eucharid parasite of Camponotus. *Ann. Ent. Soc. Amer.*, vol. 16, pp. 195–217, 2 pls.

† Parker, H. L. and Thompson, W. R., 1925. " Notes on the larvæ of the Chalcidoidea." *Ann. Ent. Soc. Amer.*, vol. xviii, pp. 384–98, pls. 26–28.

called the mermithergate . . ." (Wheeler, 1910, p. 420 and fig. 254.)

So much for a hasty sketch of some parasites of ants. The predatory enemies are of great interest in view of the significance of myrmecoidy and the theory of mimicry (see Note 26). They have been studied in considerable detail by Heikertinger and more especially by Bequaert,* who writes: " Professor Forel's aphorismic statement that 'the most dangerous enemies of ants are always other ants, just as the worst enemies of man are other men', may be true in a general way for temperate regions, where ants are not superabundant and lead a rather inconspicuous life, but it can hardly be applied to the tropics. Ants, it is true, attract comparatively few of the predaceous arthropods, against which they are very effectively armed. They form, however, a considerable portion of the diet of many reptiles, amphibians, birds and certain insect-eating mammals, some of these vertebrates being almost exclusively myrmecophagous. It may be further mentioned that many of these predaceous animals by no means confine their attacks to the smaller, more timid species of ants, but rather prefer the large-sized, powerfully defended members of the ponerine and doryline groups."

Among Arthropod predators may be mentioned the familiar ant-lion (*Myrmeleon*) and the less-known fly-maggots of the genera *Vermileo* and *Lampromyia* which have similar habits. It is remarkable enough that the ant-lion—an active six-legged larva, with powerful jaws—should capture its prey by means of a pit ambush; but that a legless maggot should accomplish the same feat is astonishing indeed. The larva of *Vermileo* does it in this manner: " The four anterior segments are slender and fimbriate on the sides; they can be curved against a ventral projection on the fifth segment so as to form a loop, with which the larva throws out the dust while burrowing its pitfall. When a small insect, usually an ant, drops into the pit it is seized and firmly held by the loop around the thorax or behind the head, the loop thus taking the place of the ant-lion's jaws." (Bequaert.)

* Bequaert, J., 1922. The predaceous enemies of ants, pp. 271–331, in Wheeler, W. M., " Ants of the American Museum Congo Expedition," *Bull. Amer. Mus. Nat. Hist.*, vol. xlv, pp. x + 1139, 45 pls., 47 maps, 133 figs.

The Calliphorid flies of the genus *Bengalia*, in India, the East Indies and tropical Africa, follow columns of foraging ants, swoop down and snatch away the flies which they are carrying.

Amphibians of many kinds are redoubtable hunters of ants. " Many of the ants found in the stomachs of amphibians [especially toads] are in an excellent state of preservation ; others are considerably improved by a thorough cleansing with caustic potash. Future collectors in tropical countries are urged never to neglect this novel manner of increasing their material." Professor Wheeler has actually described seventeen new species of ants which were obtained only in this way.

Among birds, in temperate regions, the woodpeckers are perhaps the most important feeders on ants. Thus one American species, a flicker (*Colaptes auratus*) was found to have eaten at one meal over 5,000 ants (Beal, cited by Bequaert). In the tropics very many more birds eat ants, some being almost or entirely restricted to this diet.

There are many mammals to which the term " ant-eater " has been applied, although it is not certain to what extent they subsist on " white ants " or termites, rather than true ants. The great ant-eater (*Myrmecophaga tridactyla*) of South America seems to live chiefly on termites.

It appears, indeed, according to Bequaert, that " the pangolins or scaly ant-eaters (Manidæ) . . . of the Old World tropics are the only edentates whose myrmecophagous propensities are beyond doubt ". These curious animals show many adaptations to an ant-diet. We may mention the " long, vermiform protractile tongue . . . flattened towards the tip and kept sticky with saliva abundantly produced by enormous submaxillary glands ", and the powerful gizzard-like stomach supplied with horny teeth. " The insects are swallowed whole and reach the stomach together with saliva, sand, and small pebbles often as large as a pea ; this mixture is then ground up by the peristaltic action of the stomach, whose inner walls are effectively protected by the horny pavement epithelium . . ." (Bequaert, l.c., p. 318.)

At the close of his interesting treatise, which the reader should consult for a wealth of detail, Bequaert records ants as human food in many parts of the tropics and subtropics.

Note 28.—The term "*Cercopis*" or "*Cercopidæ*" is sometimes used when Jassids or Membracids are really meant, and Belt obviously employs the name "froghopper"—which strictly belongs to Cercopids only—as equivalent to "leaf-hopper" (i.e. Jassid) or to Auchenorrhynchous Homoptera in general. True Cercopidæ, in their nymphal stages, normally dwell on the stems of plants, in a surrounding mass of frothed-up liquid (the so-called "cuckoo-spit"), or in limy tubes in similar situations. It seems to me almost certain that all general records of Cercopids as guests of ants are open to suspicion and really refer to Jassids, many of which (for instance *Acocephalus*) look extremely like true froghoppers. Lund (1831) mentions that in Brazil the chief Homoptera attended by ants are "Cicadelles", especially those of the two genera *Cercopis* and *Membracis*. He describes these insects as massing on young stems of plants and producing by their bites monstrous growths like those induced by Aphides in Europe. This description would apply more or less to Psyllids and to Membracids, but decidedly not to Cercopids.

Mann (1915) records an undetermined Cercopid as a guest *inside* the nest of a Haitian *Aphænogaster*. From his brief description, this is almost certainly not a Cercopid. It seems, therefore, that in the present state of knowledge, the Cercopids or froghoppers ought not to be listed among the ant-cows until at least one definite species has been thus authoritatively recorded.*

Note 29.—Since Lubbock's day some extraordinary discoveries have been made regarding the dealings of ants with caterpillars. Not only has the list of known myrmecophilous butterfly and moth larvæ been very greatly extended, but the relations between these and the ants have proved much more complex than those of the aphides, scale-insects, and other typical ant-cows with their hosts. We have space to touch upon only a few cases.

A number of moth larvæ—chiefly Tineids and Œcophorids—live in the nests of ants, where they act largely as scavengers, or feed on the nest material. In England

* This question has been discussed by the present writer in a paper in the *Bulletin of the Brooklyn Entomological Society*, 1928, where full citations of the above references will be found.

they have been studied chiefly by Donisthorpe (1927, pp. 108–9).

Of greater interest are the honey caterpillars—the larvæ of the Lycænids or blue butterflies. These caterpillars are provided with dorsal glands which, on solicitation by the ants, exude honey-dew which is lapped up by the milker. So far this is a typical case of trophobiosis, with the assumption, more or less unwarranted, that the caterpillars, while still in the open, are protected. Sometimes they are covered with earth or carton shelters.

In the case of *Lycæna arion*, the " large blue " of English butterfly-collectors, the association is more intimate. For long the life-history of this species was very incompletely known, but it was finally elucidated a few years ago by Chapman, Frohawk and Purefoy. During three larval stages the caterpillar lives on its food-plant—wild thyme—and then in August wanders at large till it meets an ant, which usually milks it. Other ants may do the same, but eventually " the larva hunches itself up into an extraordinary shape—the head is much retracted, the thoracic segments well up, and the posterior segments become very narrow in consequence—and the ant seizes it behind the thorax and carries it into her nest. Here the larva does not appear to attract much attention, it seeks the chambers where the ants' brood is thickest, and rests among them. It devours very many of the ants' larvæ and grows very rapidly. When full grown it spins up and pupates, in the galleries of the nest, and the imago emerges in June ". (Donisthorpe, 1927, p. 118.)

Perhaps the most interesting of all myrmecophilous caterpillars is the larva of a small Australian moth (*Cyclotorna monocentra*) belonging to a family found nowhere else in the world. In its first stage this caterpillar is parasitic upon a tree-living leafhopper which is attended and milked by the ant *Iridomyrmex sanguineus*. Later the parasite alone is carried by the ant into the nest, where it forms a cocoon and changes into the second instar—a flattened, red larva with two long tails. During the whole of the second stage this curious caterpillar lives solely on the ant-larvæ, but is eagerly solicited by the ants themselves for a secretion which it exudes from the end of the body. " If an ant is not satisfied with the quantity given out, she deliberately seizes the protruding parts and gives them a gentle nip, the mandibles can be plainly seen to press upon the juicy flesh ; if the hint is not immediately acted upon a more vigorous squeeze is given, and the tails may be gripped and pressed. This is very comical, the ants' meaning is unmistakable, and the caterpillar so thoroughly understands it, too, for a second hint never fails." (Dodd, 1912.)

Full-fed, the caterpillar leaves the nest and pupates in a cocoon which it spins on the bark of an adjacent tree. The interesting details of this curious life-history are described by Dodd.

NOTE 30.—In Europe the most highly-developed of all ant-cowkeepers are those of the genus *Lasius*. A colony of about 3,500 workers and 11,600 young, which was herding *Aphis mali* on small apple trees, received from its herd during one summer (of 100 days), according to the calculations of Eidmann, no less than a litre of honey-dew. (Eidmann, Escherich.)

The Aphides and other insects milked by the ants " pierce the integument of the plants with their slender, pointed mouthparts and imbibe the juices, which consist of water containing in solution cane-sugar, invert sugar, dextrin, and a small amount of albuminous substance. In the alimentary canal of the insects much of the sugar is split up to form invert sugar, and a relatively small amount of all the substances is assimilated, so that the excrement is not only abundant, but contains more invert, and less cane sugar." (Wheeler, 1923, p. 178.) This excrement forms honey dew, the source of which was such a puzzle to the ancients.

Specimens in the Baltic amber prove that the ants were dairy farmers many millions of years before man appeared upon the earth.

NOTE 31.—At least 2,000 species of myrmecophiles have now been described (Wheeler, 1928), and the rate at which new forms are constantly being discovered, especially in the tropics, clearly indicates that Wasmann's and Escherich's estimate of 3,000 different kinds will prove under rather than above the mark. In no other respect has the natural history of ants made more progress than in the study of myrmecophiles and their extraordinarily diverse and significant relations with their hosts.

NOTE 32.—The following is Lubbock's own note (pp. 399–402 of Appendix G, in the seventeenth edition) on this passage :—

ANT-GUESTS

Dr. Wasmann has recently published * an interesting memoir on certain of these " Ant-guests ". His observations relate exclusively to some of the beetles which live with ants.

He confirms V. Hagen's statement that the specimens of *Atemeles emarginatus* which live with *Myrmica lavinodis,* a yellow ant, are paler in colour than those which share the nests of the black *Formica fusca.* He entirely confirms the statements of previous observers that the *Atemeles* is actually fed by the ants, who also clean them just as they do their own fellows. The *Atemeles* also, on their part, perform the same kind offices for the ants. He also repeatedly saw the ants licking the bunches of golden hairs on the abdomen of the *Atemeles.*

The *Atemeles* has adopted very closely the habits of the ants with which it lives. They pair, moreover, in the nests of the ants. Still, they are not entirely dependent on their hosts, like some of the other ant-guests, but are able to feed themselves. Indeed the *Myrmicas* seem to drive them out of the nest towards the beginning of May. Dr Wasmann is disposed to attribute this to the anxiety of the ants for their young. In *Myrmica* the pupæ are naked, and he thinks the ants are afraid that the *Atemeles* would be unable to resist the temptation of eating them. In support of this suggestion, he observes that in the nests of *Formica sanguinea,* whose pupæ spin a silken cocoon and are therefore protected, he has found *Atemeles* as late as the end of June. He has not been able to satisfy himself whether the larvæ of *Atemeles* are brought up in the ants' nest or not ; but inasmuch as while the *Atemeles* are far from rare, he has only found among them a single larva which could belong to the species, and even this was not certainly identified, it seems probable that the larval stage is passed elsewhere.

Lomechusa strumosa has been recorded from the nests of *Formica sanguinea, Myrmica rubra, Formica congerens,* and *F. rufa* ; but Dr Wasmann, like V. Hagen and Forel, has

* Deutsche Entom. Zeitschrift, 1886, p. 49.

never found it except with *F. sanguinea.* It is fed by the ants in the same manner as *Atemeles,* and has very similar bundles of golden hairs on the abdomen, which are licked by the ants like those of *Atemeles.* While, however, the ants seem to communicate with the *Atemeles* mainly by means of the antennæ, in the case of *Lomechusa* the parts of the mouth are brought more into play. He has found *Lomechusa* in the ants' nests up to the end of June.

Dinarda dentata is a still more frequent inmate in the nests of *F. sanguinea,* but plays a very different part. The ants seem indifferent to them, and when they take any notice it is of an unfriendly character. Nor can this be wondered at, for according to M. Wasmann the principal food of the *Dinardas* consists of any ant which may chance to die, or any other weak insect which falls in their way. The ants seem thoroughly to distrust them, and it is curious that they should be tolerated. Grimm, indeed, thought he had seen ants licking the *Dinardas,* as they do *Atemeles* and *Lomechusa.* Wasmann, however, considers that this was a mistake; at any rate he has never seen anything of the kind. If an ant meets a *Dinarda* she either treats it with indifference or threatens the beetle with her jaws, and the *Dinarda* then raises its abdomen, which appears always to drive away the ant. It is possible that the *Dinarda* has the power of producing an odour distressing to the ants, or perhaps they eject poison like the *Formicas* themselves. They seem always to remain in the nests of the ants, and pass through their transformation in them. *Formica sanguinea,* like *F. rufa* and *F. congerens,* changes its nest periodically twice a year; such, at least, is said to be the case on the continent; I am not aware whether the same habit has been observed in this country. The summer nests are looser and opener, the winter ones lower and more compressed. In their migration from one nest to the other, which are occasionally at some distance apart, the ants are accompanied by the *Dinardas.* On one occasion, when the ants were flitting, Dr Wasmann in twenty minutes captured among them thirteen specimens of *Dinarda*; while under other circumstances he never saw one outside the nest.

Hetærius ferrugineus, belonging to a totally different family of beetles, the Histeridæ, and which inhabits the nests of *Polyergus rufescens, Formica sanguinea, F. pressilabris, F. fusca, F. rufibarbis, F. rufa, F. exsecta, Lasius niger,* and *Tapinoma erraticum,* appears to agree in its habits with *Dinarda,* and to devour dead and wounded ants, as also do the Myrmedoniæ.

Dr Wasmann confirms entirely my observations, in opposition to the statements of Lespès, that while ants are deadly enemies to those of other nests, even of the same species, the domestic animals, on the contrary, may be transferred from one nest to another and are not attacked.

He justly observes that, no doubt, many interesting discoveries are in store for us as to the relations between ants and their guests. The marvellous and grotesque antennæ of the Paussidæ will doubtless, one of these days, tell a wonderful story to some patient and fortunate observer.

Editor's Note.—According to Wheeler (1910, p. 401) the antennæ of the Paussidæ, with their joints fused and dilated, "are used as handles, by means of which the ants can carry or drag their guests about the nest."

Note 33.—The following is Lubbock's own note (pp. 402–3 of Appendix G, in the seventeenth edition) on this passage :—

Mimicry among Ants

Professor C. Emery has published in the *Bull. della Soc. Ent. Italiana,* 1886, a short, but interesting note on the habits of *Camponotus lateralis.* Of this species there are two varieties : one black, like its nearest allies ; the other red, with the abdomen and part of the thorax black. They live in small colonies, and make expeditions up trees to collect honey-dew from the Aphides. The black type (*C. foveolatus,* Mayr ; *C. ebeninus,* Emery) sometimes goes in troops, but generally a few join the troops of other black ants, such as *Formica gagates* and *Camponotus æthiops.* Professor Emery suggests that, their numbers being small and their sight not very good, they find it convenient to accompany other ants which live in larger communities, and that they perhaps escape detection from the similarity of colour.

This suggestion derives some support from the fact that the red variety accompanies in a similar manner the troops of *Cremastogaster scutellaris,* which is red and black, and at first sight curiously like the red variety of *C. lateralis*. *Cremastogaster scutellaris* lives in immense communities among the pine woods along the shores of the Mediterranean, and is, as I know to my cost, a very pugnacious species. Professor Emery suggests that the black form of *C. lateralis* is the original type, resembling as it does its nearest congeners ; and that the red variety has the advantage, from its similarity to *Cremastogaster scutellaris*, of using that species as its guide, and of sharing, undetected, in the produce of its flocks and herds. Professor Emery observes that he only suggests this explanation. The facts he mentions are very interesting, and it is to be hoped that he will continue his observations.

NOTE 34.—The following is Lubbock's own note (pp. 398–9, of Appendix G, in the seventeenth edition) on this passage :—

ON THE RELATION BETWEEN *Formica sanguinea* AND ITS SLAVES

It is well known that *Polyergus rufescens* is entirely dependent on its slaves. Huber long ago found that this ant will starve in the midst of plenty, and will not even put food into its own mouth. I have shown that isolated specimens will live for months if they are allowed a slave for an hour or so every two or three days to clean and feed them. It is said, on the contrary, that our only slave-making species, *Formica sanguinea*, can manage without slaves. Indeed, it appears that nests are sometimes found in which there are mistresses alone, entirely without slaves. Forel thinks that he has observed in such nests generally a larger proportion of small individuals than in nests which possess slaves. This would be interesting as tending to show that in such nests the young are less well nourished than when they have slaves to attend upon them.

The question remains, of what advantage are the slaves to the *F. sanguinea* ? Forel says, I do not quite understand why, " Je ne veux pas trop rechercher le motif qui pousse les *sanguinea* a se faire presque toujours des esclaves." " Peut-être," he adds, " le sentiment de leur force, et le désir de travailler moins, pour faire plus à leur aise la chasse aux *Lasius flavus* et *L. niger*, est-il le mobile qui les pousse à cet acte. Celui-ci leur serait peu à peu devenu plus ou moins instinctif puisqu'il était avantageux à la conservation de leur espèce.'' This suggestion seems very probable, and may be partially correct ; it is not, however, I think, a complete explanation. I have had under observation several nests of *F. sanguinea.* One of them I owe to the kindness of M. Forel himself, who sent it to me in June, 1882. There was no queen, and, though the nest was very healthy, of course the numbers gradually diminished. At the beginning of January, 1886, the last slave died, and there then remained only about fifty *F. sanguinea.* Under these circumstances the *F. sanguinea* began to die off rapidly ; by the middle of the year only six remained alive, and these, no doubt, would not have survived long. On July 1, I got some pupæ of *F. fusca* and placed them outside the nest. The *sanguineas* soon discovered them, carried them into the nest, and from that day until December, 1887, more than six months, there was only one other death. [Two of the *F. sanguinea* are still (August, 1888) alive.] Although then it may be true, as to which I express no opinion, that there are nests of *F. sanguinea* without slaves, still this observation seems to indicate that the slaves perform some important function in the economy of the nest. It still remains to be determined in what exactly this function consists.

Note 35.—Since Lubbock wrote, three or four other forms of *Strongylognathus* have been discovered in Europe and described as species, sub-species, or varieties. See Note 36.

Note 36.—The habits of *Strongylognathus testaceus* are still not completely known, but the study of a number of other genera discovered since Lubbock, has brought to light an exceedingly interesting behaviour series, which is believed to represent also an evolutionary sequence, from ordinary predatism, leading on through slave-making to temporary and finally permanent social parasitism. The species of *Strongylognathus* have been called "degenerate slave-makers", and *S. testaceus* touches the bottom of this degradation since it has become a definite parasite in the colonies of *Tetramorium.* Its "workers are so much reduced in numbers as to represent a mere vestige of their caste. Forel is, therefore, of the opinion that they are on the verge of disappearing and leading to a condition in which the species is represented by males and females only. It is certain that these workers no longer make spontaneous forays on alien colonies of *Tetramorium.* When the latter are brought near a mixed colony and a conflict ensues, the *testaceus* endeavour to kill the strange workers, but are too feeble to pierce their armour, and, if the mixed colony is victorious, this is due to the efforts of the host workers. The *testaceus,* though able to excavate and to feed independently, contribute little or nothing to the structure of the nest and probably obtain most of their food from the tongues of the *Tetramorium.* The broods of both species are cared for by the host, since the parasites have ceased to interest themselves in the education of their own young. Unlike many parasitic ants, *S. testaceus* is often found in vigorous and populous colonies of the host species. The flourishing condition of such colonies, . . . must be due either to the retention of the *Tetramorium* queen or to adoption of the *Strongylognathus* queen at a very late stage in the development of the colony. That we must accept the former alternative is proved by the following observations: In Bohemia, Wasmann found a large mixed colony which contained 15,000–20,000 *Tetramorium,* some thousand *Strongylognathus* and pupæ of both species. About 70 per cent of the pupæ were males and females of the parasitic species, the remainder were worker pupæ, and there were two large male pupæ of the host. This nest contained a fertile queen of *Tetramorium* and one of *Strongylognathus,* living side by side. During June, 1907, Professor Forel and I were able to confirm this discovery". (Wheeler, 1910, pp. 490, 491.)

Wasmann thought that these mixed colonies arise through an alliance between a *testaceus* and a *Tetramorium* queen, about to found a colony, and later evidence has supported this view, though the matter is not entirely settled. Forel says (1928, i, p. 536): "The fact that the nuptial flight of the two species takes place at exactly the same time adds weight to the same argument."

The mixed colonies practically never produce male and female offspring of the host species, but only workers, though large numbers of *Strongylognathus* sexed individuals are reared. Forel suggests "that the reason for this is the smaller amount of effort required to feed and rear the little *S. testaceus* brood", instead of "their own enormous queens and males, the larvæ of which they undoubtedly devour or neglect, as they do in the case of all that seems to be superfluous ".

Harpagoxenus (formerly known as *Tomognathus*) is another of the degenerate slave-makers. The habits of *Harpagoxenus americanus* have been recently studied by Creighton,* who writes that " while much remains to be done it is now possible to sketch the ethology of *H. americanus* ; a hasty sketch to be sure, with many missing features hypothetically supplied, but at least a beginning. In this picture we see the fertilized *Harpagoxenus* queen entering a *Leptothorax* nest by force. Having driven away or killed the original owners of the brood, she appropriates this, tends it and is in turn tended by the resulting *Leptothorax* workers, until in time there arises a mixed colony. When the colony is well established the dulotic instinct manifests itself in the *Harpagoxenus* workers. These gain entrance to some *Leptothorax* nest after a long struggle in which their greater hardiness and superior size finally enables them to kill or intimidate the *Leptothorax* workers. If the external conditions are favourable the raid is carried to a successful conclusion, and the brood of the pillaged nest is carried back to the mixed colony. If the return of the raiders is rendered impossible then a fragmentary mixed *Harpagoxenus-Leptothorax* colony results."

"The slave raids of *Harpagoxenus* show none of the organization and spirit so characteristic of those of *Polyergus*. They fall far short even of the lesser degree of co-operation exhibited by *F. sanguinea*. Nevertheless they are of great interest, since they appear to be the last manifestation of a vanishing character. They show the decay of dulosis and foreshadow a state of abject parasitism. During the progress of a raid the *Harpagoxenus* workers and their slaves cluster about the entrance of their nest in a manner suggestive of *Polyergus*, but with this the similarity ends. There is no rapidly moving phalanx of raiders, no concentration about the entrance of the raided nest, no frantic activity to enlarge the entrance. The *Harpagoxenus* leave their nest singly and amble awkwardly and uncertainly to the nest of their victims. Only once did I see more than one *Harpagoxenus* leave the nest at the same time. On one occasion a column of three departed for the

* Creighton, W. S., 1927, " The slave-raids of *Harpagoxenus americanus*," *Psyche*, Boston, xxxiv, pp. 11–29.

Leptothorax nest. However, this column broke up almost at once and was, I believe, purely fortuitous. On arriving at the *Leptothorax* nest, the *Harpagoxenus* wastes no time in preliminaries, but enters at once. Having secured a larva or pupa, it emerges as quietly as it entered, and returns with its burden to its own nest. Quite often they lose their way, and I have seen a number of them captured by small spiders while raiding. The action of *Harpagoxenus* after it enters the raided nest could not, of course, be followed in the field. However, observation of ants in artificial nests show [sic] that the brood is obtained by force and not by stealth, although indeed, the action of the *Leptothorax* during a raid furnishes ample evidence that this is the case." (l.c., p. 14.)

So much for the degenerate slave-makers. Let us return to our evolutionary series, which must be considered in certain of its other members if we are to understand the position of such a workerless parasite as *Anergates* whose life-history is described in the next note.

"In 1904," Wheeler "detected another method of forming mixed colonies, which I called temporary, although I might have called it acute, social parasitism. It is practised by a number of ants, especially by several North American species of Formica that have unusual queens. In some species they are peculiarly coloured or furnished with long yellow hairs, in others they are extremely small, smaller even than the largest workers. . . . The young queen of these ants enters the nest of another Formica belonging to the *fusca* or *pallide-fulva* group and is very apt to be adopted, probably on account of her smaller size or other physical attractions. The fate of the host queen in such invaded nests has not been ascertained, but she is probably killed by her own workers. The parasite then proceeds to produce her brood, which is reared by the host workers, and a mixed colony results. As there is no inclination on the part of the queen's offspring to plunder other nests of the host species, and as all the host workers die off in the course of a few years, a pure colony of the parasitic species is left behind and may grow to be very populous and aggressive, without showing any signs of parasitic origin—a beautiful analogue of some human institutions, which after starting in humble and cringing parasitism have come to acquire during the centuries a most exuberant and insolent domination. Our common mound-building ant (*Formica exsectoides*) is one of these successful temporary parasites, which starts its opulent colonies with the aid of the ubiquitous *F. fusca* var. *subsericea.* Since my observations were published, several European Formicas, including the well-known mound-building *rufa*, and ants of certain other genera (Lasius, Bothriomyrmex, Aphænogaster, etc.), in various parts of the world have been found to be temporary social parasites. One of the most interesting of these is the Dolichoderine *Bothriomyrmex decapitans* which Santschi observed in Tunis. The young queen, on descending from her marriage flight, wanders about on the ground till she finds the nest of a *Tapinoma nigerrimum* colony, when she permits herself to be seized and 'arrested' by its workers. These then proceed to drag her into their burrow by her legs and antennæ. After entering the nest, the parasite may be attacked from time to time by the workers, but she takes refuge on the brood or on the back of the larger Tapinoma queen. In either of these positions she seems to be quite immune from attacks, probably because her own odour is overlaid by that of the brood or the host queen. Santschi observed that the parasite often spends long hours on the back of the Tapinoma queen, and that while in this position she busies herself with sawing off the head of her host! By the time she has accomplished this cruel feat, she has acquired the nest-odour and is adopted by the Tapinoma workers in the place of their unfortunate mother. The parasite thereupon proceeds to keep them busy bringing up her brood. They eventually die of old age, and the nest then becomes the property of a thriving, pure colony of *Bothriomyrmex decapitans*." (Wheeler, 1923, pp. 213–15.)

NOTE 37.—"No less than fourteen genera and seventeen species of ants, from various parts of the world, may be classed as permanent, or chronic social parasites." (Wheeler.) They have all lost the worker class, but whereas some show little structural alteration and are alike in both sexes, others exhibit marked degenerative modification. In the latter group is *Anergates*, the economy of which—such a mystery to Lubbock—has since been more or less completely elucidated.

" The young queens " of all these forms " enter into the nests of other ants and secure adoption, like the queens of the temporary social parasites. The host queen seems to be regularly assassinated by her own workers. At least this has been observed by Santschi (Forel, 1906) in the case of *Wheeleriella santschii*, which lives in the nests of the common North African *Monomorium salomonis*. After fecundation the *Wheeleriella* queen roams about over the surface of the soil in search of a Monomorium nest. When near the entrance of one of them she is ' arrested ', to use Santschi's expression, by a band of Monomorium workers, which tug at her legs and antennæ and draw her into the galleries. Sometimes she may be seen to dart suddenly into the entrance of her own accord, and is arrested within the nest. There are no signs of anger on the part of the Monomorium, and she is soon permitted to move about the galleries unmolested. The workers then begin to feed and adopt her, and in the course of a few days she lays her first eggs, which are accepted and cared for by the host. The parasite pays no attention to the much larger Monomorium queen, but the latter is eventually assassinated by her own workers. Other species, like the famous *Anergates atratulus* (Fig. 78) of Europe, the recently discovered *Anergatides kohli* (Wasmann, 1915) of the Congo, and *Bruchomyrma acutidens* of the Argentine (Santschi, 1922) are much more highly modified, and represent the last stages of parasitic degeneration. In Anergates, which lives with *Tetramorium cæspitum*, and has been studied by a number of investigators, the queen is small and winged, but after deälation and adoption her gaster swells enormously with eggs till she somewhat resembles an old termite queen. The male is wingless and pupa-like, and unable to leave the nest. Mating therefore takes place between brothers and sister (' adelphogamy ' of Forel). The conditions in Anergatides and Bruchomyrma which live in the nests of Pheidole species, are somewhat similar. In all these workerless parasites the offspring of the intrusive queen are, of course, all males and females, and are produced within the lifetime of the host workers. The colonies are therefore mixed throughout their existence which is necessarily terminated by the death of the host." (Wheeler, 1928, pp. 294–5.)

" Raines' remarks [on physiological interrelations between hosts and parasites] are very suggestive also in connection with the much-discussed question of the phylogenetic relations of the three types of behaviour exhibited by the dulotic, temporary, and permanent social parasites among the ants. They obviously form a series comparable with the predatory (synechthran), synoeketic, and symphilic series among the myrmecophiles and the ants which form compound nests with other Formicidæ. All investigators agree that the workerless, permanent parasites represent the final, degenerate and evanescent evolutionary stage in the series of social parasites, but opinions are divided in regard to the initial, or primitive stage. Wasmann and Piéron (1910) contend that it is represented by the temporary parasites, and would derive their behaviour from that of queen ants, which after fecundation, seek and secure adoption in colonies of their own species (secondary pleometrosis). From temporary parasitism, according to these authors, both the dulotic and permanently parasitic behaviour are to be derived. Viehmeyer, Emery, and Brun, and I contend, however, that predatory behaviour of the type exhibited by *Formica sanguinea* more probably represents the initial stage and that the conciliatory, temporary and finally abject, permanent parasitism represent natural ulterior developments of this violent, or aggressive relation between host and parasite. This contention is supported, first, by the general considerations that parasitoidism and parasitism are evidently derived from predatism among a great many solitary insects and that this sequence obtains also among the myrmecophiles, the social parasites among the bees, and degenerate slavemakers (e.g. Strongylognathus), the ants which form compound nests, etc.; and second by the more special consideration that the queens of certain temporary parasites, with large queen, e.g. *Formica rufa*, sometimes behave like *F. sanguinea* when establishing their colonies and the species with small queens, red or yellow coloration and trichomes, are obviously derived forms." (l.c., pp. 297–8.)

Note 38.—Lubbock builded better than he knew in pointing out this interesting analogy. His knowledge of ant biology permitted him to separate the three principal types of hunting, cattle-keeping, and agricultural ants, but his acquaintance with ant phylogeny was not sufficient to indicate how far this series is a developmental one. Thus he instances *Formica fusca* as a species still at the hunting stage. But the genus *Formica* is morphologically one of the most highly evolved.

Comparative morphology points to certain groups as containing much more primitive species, approximating more nearly to the hypothetical ancestral form, and it is precisely " the ants belonging to the oldest and most primitive subfamilies, the Ponerinæ, Dorylinæ, and Cerapachyinæ and also to many of the lower genera of Myrmicinæ, (which) feed exclusively on insects and therefore represent the hunting stage of human society ".

" The pastoral stage is represented by a great number of Myrmicine and especially of Formicine and Dolichoderine ants which live very largely on ' honey-dew '. A very few species of Ponerine ants also keep ' cows '.* This secretion is obtained either directly from plants—from small glands or extrafloral nectaries—or, in much greater abundance, from insects—chiefly aphides, scale-insects, and leafhoppers (Homoptera)—which they ' milk ' and tend.

" The harvesting ants can hardly be regarded as true agriculturalists, because they neither sow nor cultivate the plants from which they obtain the seeds. Yet there is a group of ants which may properly be described as horticultural, namely, the Attiini, a Myrmicine tribe comprising about 100 exclusively American species . . ." (Wheeler, 1923, p. 182.) Every species of these ants cultivates its own special kind of fungus, and no other is allowed to grow in its elaborate gardens. Under the horticultural care of the smallest workers, and not when the ants are kept away, the fungi produce " abundant clusters of small spherical swellings, the bromatia, which are eaten by the ants and fed to their larvæ ". When the virgin queen departs to begin a new colony, her infrabuccal pocket is packed with fragments of the fungus, which she casts on the floor of the new chamber, manures with her excrement, and even with some of her first eggs, mashed up. Other eggs hatch into larvæ which feed on the now growing fungus, and when adult take over its charge.

There is thus a very striking analogy between the social evolution of ants and that of man. One of the greatest

* See Myers, *Bull. Brooklyn Ent. Soc.*, 1928.

differences lies in the time required for the respective development of the two societies. "In order that we and the impatient reformers in our midst may experience the proper feeling of humility let us now compare the age of man and his society with that of the ants. During the Oligocene and early Miocene, while these insects, together with the uncouth, primitive mammals, represented the dominant animal life of the plains and forests of the globe, the early Primates were just splitting into two tribes, one of which was destined to produce the modern apes, the other the Hominidæ, or humans. Our ancestors were probably just forsaking that life among the tree-tops which, as F. Wood Jones has shown, has left its ineffaceable impress on all the details of our anatomy. A large part of the diet of these early Hominids and their immediate ancestors probably consisted of those same ants which had already developed a co-operative communism so complete that in comparison the most radical of our bolsheviks are ultra-conservative capitalists. By a hundred thousand years ago our ancestors had reached the stage of Neanderthal man, whose society was probably somewhat more primitive than that of the Australian savage of to-day. And so far as the actual, fundamental, biological structure of our society is concerned and notwithstanding its stupendous growth in size and all the tinkering to which it has been subjected, we are still in much the same infantile stage. But if the ants are not despondent because they have failed to produce a new social invention or convention in 65 million years, why should we be discouraged because some of our institutions and castes have not been able to evolve a new idea in the past fifty centuries?" (Wheeler, 1923, pp. 8–9.)

Note 39.—Wheeler (1910, p. 536) writes: "There has been much discussion as to whether or not coöperation among ants extends to the succouring of companions in danger or distress. Reuter (1888) claims to have found positive evidence of such acts of sympathy, but the observations of most myrmecologists have yielded only doubtful results. My own observations are negative, except in a single instance. Several years ago I kept a large colony of *Eciton schmitti* in a Lubbock nest surrounded by a water moat. Workers repeatedly fell into the water and on several occasions I saw other workers reach down and pull them out. Forel, Lubbock, and Wasmann relate instances of ants nursing and caring for crippled or mutilated companions. But if we reject all such observations [including those described before our quotation begins.—Ed.] as too infrequent or doubtful to have any value, there still remain a great many easily observed cases that can be explained only on the supposition that ants respond quickly by imitating the purposeful activities which they perceive in their nest-mates. The stimulus in these cases would seem to be highly individualized, to use Driesch's expression, and entirely unlike those which call out reflex and instinct actions."

We shall quote one example of this care of the injured from Wasmann, who has emphasized its importance in his arguments designed to show the superior psychical endowment of ants as compared with the highest mammals and the impossibility of any evolutionary sequence from the latter to man. He writes,* "Ants as 'sick nurses' seemed so strange to me, that I was unwilling to admit the fact, until I observed it myself. The first time was on 16th March, 1895. I had replaced in the main part of the aforementioned nest a *sanguinea* which had been paralysed in one of the narrow glass tubes by an ejection of formic acid, and was scarcely able to move in spite of her convulsive efforts. At first her companions, on approaching, appeared to take no notice of her distress. Yet, after a short time, they began to examine her with their feelers, and then carried her to another part of the nest where the greater number were assembled. In this place the sick ant was lying for a whole day, surrounded by a number of masters and slaves (*fusca*) which, mostly in groups, busied themselves about her. They licked her carefully, turned her over and licked her again, examined her with their feelers, and licked her once more. This method of medical treatment was attended with complete success. The patient had fully recovered by the next day, whilst without nursing she would probably have perished, as is generally the case with ants paralysed by poison."

Note 40.—The following is Lubbock's own note (pp. 411–15 of Appendix G in the seventeenth edition) on this question :—

* Wasmann, E., 1905, *Comparative Studies in the Psychology of Ants and of Higher Animals*, St. Louis and Freiburg, 2nd ed., p. 27.

Recognition of Friends

In the interesting memoir already cited Forel says :—" Lubbock (l.c.) a cru démontrer que les fourmis enlevées de leur nid à l'état de nymphe et écloses hors de chez elles étaient néanmoins reconnues par leurs compagnes lorsqu'on les leur rendait. Dans mes ' Fourmis de la Suisse ' j'avais cru démontrer le contraire. Voici une expérience que j'ai faite ces jours-ci : le 7 août, je donne des nymphes de *Formica pratensis* près d'éclore à quelques *Formica sanguinea* dans une boîte. Le 9 août quelques-unes éclosent. Le 11 août, au matin, je prends l'une des jeunes *pratensis* âgée de deux ou trois jours seulement et je la porte à la fourmilière natale dont elle était sortie comme nymphe seulement 4 jours auparavant. Elle y est fort mal reçue. Ses nourrices d'il y a 4 jours l'empoignent, qui par la tête, qui le thorax, qui par les pattes en recourbant leur abdomen d'un air menaçant. Deux d'entre elles la tinrent longtemps en sens inverse, chacune par une patte en l'écartelant. Enfin cependant on finit par la tolérer, comme on le fait aussi pour de si jeunes fourmis (encore blanc jaunâtre) provenant de fourmilières différentes. J'attends encore deux jours pour laisser durcir un peu mes nouvelles écloses. Puis j'en reporte deux sur leur nid. Elles sont violemment attaquées. L'une d'elles est inondée de venin, tiraillée et tuée. L'autre est longtemps tiraillée et mordue, mais finalement laissée tranquille (tolérée ?). On m'objectera l'odeur des *sanguinea* qui avait vécu 4 jours avec la première et 6 jours avec les deux dernières. A cela je répondrai simplement par l'expérience de la page 278 à 282 de mes ' Fourmis de la Suisse ', où des *F. pratensis* adultes séparées depuis deux mois de leurs compagnes par une alliance forcée avec des *F. sanguinea*, alliance que j'avais provoquée, reconnurent immédiatement leurs anciennes compagnes et s'allièrent presque sans dispute avec elles. Je maintiens donc mon opinion : les fourmis apprennent à se connaître petit à petit, à partir de leur éclosion. Je crois du reste que c'est au moyen de perceptions olfactives de contact." *

I have, however, repeated my previous observations with the same results.

* Auguste Forel, " Expériences et Remarques critiques sur les Sensations des Insectes," *Recueil Zool. Suisse*, tome iv (1887), pp.179–80.

At the beginning of August, I brought in a nest of *Lasius niger* containing a large number of pupæ. Some of these I placed by themselves in charge of three ants belonging to the same species, and taken from a nest which I have had under observation for rather more than ten years. On 28th August, I took twelve of the young ants, which in the meantime had emerged from the separated pupæ, selecting some which had all but acquired their full colour. Four of them I replaced in their old nest, and four in that from which their nurses were taken.

At 4.30.	In their own nest none were attacked.
	In their nurses' nest one was attacked.
5.	In their own nest none were attacked.
	In their nurses' nest all four were attacked.
8.	In their own nest none were attacked.
	In their nurses' nest three were attacked.

The next day I took six more and marked them with a spot of paint as usual, and at 7.30 replaced them in their own nest.

At 8 I found 5 quite at home. The others I could not see, but none were attacked.

8.30	,,	5	,,	,,	,,
9	,,	3	,,	,,	,,
10	,,	4	,,	,,	,,
11	,,	5	,,	,,	,,
12	,,	3	,,	,,	,,
1	,,	3	,,	,,	,,
4	,,	4	,,	,,	,,
7	,,	1	,,	,,	,,
9	,,	2	,,	,,	,,

The next morning I could only see two, but none were being attacked and there were no dead ones. It is probable that the paint had been cleaned off the others, but it was not easy to find them all among so many. At any rate none were being attacked nor had any been killed.

These observations, therefore, quite confirm those previously made, and seem to show that if pupæ are taken from a nest, kept till they become perfect insects, and then replaced in the nest, they are recognized as friends.

When we consider the immense number of ants in a nest, amounting in some cases to over 500,000, it is a most remarkable fact that they all know one another. If a stranger, even belonging to the same species, be placed among them, she will be at once attacked and driven out of the nest. Nay, more, I have already shown that they remember their friends even after more than a year's separation, and that it is not by any sign or password, because even if rendered intoxicated, so as to be utterly insensible, they are still recognized. As regards the mode of recognition, Mr. McCook considers that it is by scent, and states that if ants are more or less soaked in water, they are no longer recognized by their friends, but are attacked. He mentions a case in which an ant fell accidentally into some water :—

"She remained in the liquid some moments, and crept out of it. Immediately she was seized in a hostile manner, first by one, then by another, then by a third ; the two antennæ and one leg were thus held. A fourth one assaulted the middle thorax and petiole ; the poor little bather was thus dragged helplessly to and fro for a long time, and was evidently ordained to death. Presently I took up the struggling heap. Two of the assailants kept their hold ; one finally dropped, the other I could not tear loose, and so put the pair back upon the tree, leaving the doomed immersionist to her hard fate."

His attention having been called to this, he noticed several other cases, always with the same result. I have not myself been able to repeat the observation with the same species, but with two at least of our native ants the results were exactly reversed. In one case five specimens of *Lasius niger* fell into water and remained immersed for three hours. I then took them out and put them into a bottle to recover themselves. The following morning I allowed them to return. They were received as friends, and though we watched them from 7.30 till 1.30 every hour, there was not the slightest sign of hostility. The nest was moreover placed in a close box, so that if any ant were killed we could inevitably find the body, and I can therefore positively state that no ant died. In this case, therefore, it is clear that the immersion did not prevent them from being recognized. Again, three specimens of *Formica fusca* dropped into water. After three hours I took them out, and after keeping them by themselves for the night to recover, I put them back into the nest. They were unquestionably received as friends, without the slightest sign of hostility, or even of doubt. I do not, however, by any means intend to express the opinion that smell is not the mode by which recognition is effected.

[Editor's Note.—It seems now generally agreed that ants recognize their nest-mates by means of the contact-odour sense seated in the antennæ. To explain, however, not only recognition of fellows, but also numerous other activities "we must suppose", with Wheeler (1910, p. 510) "that ants have not only extremely acute powers of odor-discrimination, but no less extraordinary powers of odor-association. Even the degenerate human olfactories can detect the different species and in some cases even the different castes of ants (*Eciton*) by their odors, but these insects carry the discrimination much further. They not only differentiate the innate odors peculiar to the species, sex, caste and individual and the adventitious or 'incurred' odors of the nest and environment, but, according to Miss Fielde, they can detect 'progressive odors' due to change of physiclogical condition with the age of the individual. She believes that 'as worker ants advance in age their progressive odor intensifies or changes to such a degree that they may be said to attain a new odor every two or three months'."

Forel, by a striking experiment, long ago proved the dependence of recognition upon the topochemical sensations of the antennæ. He says (quoted 1928, vol. i, p. 198): "I put into the same phial ants of entirely different species and even genera (*Camponotus ligniperdus*, *Tapinoma erraticum*, and various species of *Lasius* and *Formica*), from all of which I had cut off both antennæ. They intermingled completely with one another, making no distinction; I saw *Lasius* licking *Formica* and *Camponotus*; I even observed the beginning of a regurgitation between a *Lasius fuliginosus* worker and a *C. ligniperdus* worker. These ants did not become aware of the presence of the honey until their mouths happened to get immersed in it; then they began to eat, although clumsily, and in the end they always stuck to it by their front legs, which they were trying to use as probing instruments in the stead of their antennæ. These ants made it clear to me that their intelligence had not suffered in any way, but that they were no longer susceptible to fine sensations. They strove their utmost to take their bearings with their legs, palpi and head, forcing these organs to make unaccustomed movements. When they encountered one another they began mutual probings with their palpi and front legs, and evidently finished, judging by what we have described, by supposing one another to belong to the same formicary. On some occasions, however, I observed certain very emphatic gestures of suspicion, such as a sudden recoil, with threatening movements of the mandibles, but that was not repeated."

NOTE 41.—Here are inserted in the text, portions of pages 366, 367, 368, 373, of Appendix D of the seventeenth edition.

NOTE 42.—It is now generally admitted that ants are able to communicate effectively with their fellows, but there is considerable discussion as to what they can communicate and what not. Wasmann, whom, as Forel justly remarks, no one could accuse of wishing to humanize the ants, has even gone so far as to compile a vocabulary of the antennal "language". According to Brun and to Forel (1928, i, p. 240), "the difference between the various signs of the antennal language lies chiefly in their violence or calmness, their lightness, and their length or shortness, with the frequency of the pauses between them. These signs also differ according to whether they are struck on the forehead, the sides of the head, the body or the antennæ themselves of the companion to which the ant addresses herself. There are also many transitions between these various signs. Needless to say, the nature and form of smells likewise plays a large part in antennal language. It is only by long and patient observation that we men can achieve an *approximate* reading of this interesting ant-language . . . Again, as Huber has already shown, ants do not talk exclusively with their antennæ. Particularly when they are excited, they strike the bodies of others with their heads. When they are asking for food, they also caress with their front legs the companion which is regurgitating honey, somewhat in the manner of dogs. When a companion which has been warned of a danger, or which has to be transported, turns 'the deaf ear' they seize hold of her by the legs and drag her away. The *Camponotus* in their wooden nests strike the walls with the abdomen and the head to signify danger ; I have seen and heard them do so many times, for this noise is clearly perceptible to the human ear."

Wheeler (1910, p. 535) has "also interpreted the rapid antennary vibrations, the minatory divarication of the jaws, the butting with the head, the supplicatory posture of the body, the striking of the floor of the nest with the gaster, etc., as so many signs which may be understood and acted on by the ants". It must, however, be remembered that, "of course, all the signs or signals employed by ants and other animals in conveying their impressions to other members of their respective species are concrete and instinctive, or what Bergson calls 'adherent', and not 'movable' or rational signs like those of language and mathematics."

Concerning the red tree-ant (*Œcophylla smaragdina*) of the eastern tropics, already so famous for its employment of its own larvæ as living shuttles in nest-weaving, Hingston * has written that "most ants communicate danger by touch ; this ant does so by means of sight. When it is alarmed it stands still, gets into an alarm attitude, with head and thorax raised from the leaf and antennæ thrust up into the air. Then it proceeds to make jerking movements, vibrates its antennæ, flicks its abdomen. Another ant sees the attitude and jerkings. It proceeds to do the same. A third ant follows, then a fourth, and the news spreads through the whole nest."

In another most interesting contribution the same observer describes various degrees of efficiency in communication among Indian ants, in what he believes to represent an evolutionary series.† He writes, "Let us first consider it in the finished state. We can observe it thus in many kinds of ants. *Phidole* (sic) *indica*, for example, habitually communicates, a worker invariably running back for assistance whenever a capture is made. *Camponotus compressus* has a similar power, but makes use of it only on special occasions, such as when it is unable to shift its load . . . *Phidole indica* will best exemplify the act. As soon as a worker discovers

* Hingston, R. W. G., 1928, "The Habits of *Œcophylla smaragdina*," *Proc. Ent. Soc. Lond.*, 2, pp. 90–4.

† "The evolution of the faculty of communication in ants." *Rep. Proc. Fifth Ent. Meeting, Pusa* (1923), Calcutta, 1924, pp. 289–95.

an insect, its first act is to make a superficial exploration, then, finding the insect too heavy for transportation, it hastens at full speed back to the nest. It plunges straight into the entrance, and in a few seconds after it has disappeared, a dense army of excited workers comes pouring hurriedly out through the gate. Without the slightest hesitation they hasten outwards, follow back along the track of the discovering worker, and, as a rule without encountering any special difficulty, come on the treasure which the first worker had found.

"Such is the occurrence as we ordinarily see it, but there are certain details with respect to its production which demand our special note. The first is that the worker which brings back the news does not act as a leader to the issuing army, for the army will often advance in front of the discoverer, or, if the discoverer is captured at the moment of its exit, the army will still be able to find the place. The second point is that the army, in its outward progress, retraces the track of the discovering ant; and the third detail is that the army recognizes this track by means of the faculty of smell. In this act we see the height of the communicating efficiency. A worker arrives, proclaims the news, and, without the necessity of its further co-operation, the army secures the spoil.

"Bearing in mind this manifestation of the instinct in *Phidole*, let us turn now to some other species for instruction in the manner by which it has evolved.

"The first species to consider is *Camponotus sericeus*. It possesses no such elaborate power of calling out an army of workers to its aid. But it often displays a more instructive performance, which illustrates, I believe, the primitive foundation on which this faculty of communication is based. It is a common occurrence to see a pair of workers making their exit from this ant's nest. The first is clearly the leader of the pair; the second is being led. . . . They never change their respective positions; the second worker keeps close up to and immediately behind the first. It scarcely ever falls more than half an inch behind, and it follows exactly in the footsteps of its leader through every turn and inclination that occurs. . . . The one in rear continually makes little forward rushes so as to touch the tail of the one in front. . . . The leader too assists in maintaining connection. It moves at less than its ordinary speed and in a rhythmical succession of jerks. . . .

"In this we have the simplest form of communication and the most rudimentary example of a call for aid. It is simple in the first place owing to the number engaged; it is a case of just one ant bringing forth another; there is no attempt at a straggling troop, still less at a multitudinous swarm. In the second place it displays only the weakest of links; if the follower happens to fall only an inch behind its leader, then the connecting bond between the two is severed and the follower can no longer pursue its course. In the third place we notice the mechanism of communication; it is the simplest and most primitive of all possible kinds, merely the ordinary and intelligible instrumentality of touch. Lastly, we must observe, so undeveloped is the instinct, that the leader has frequently to assist the progress by waiting until its follower, which often goes astray, has regained its previous position in rear."

In *Camponotus paria* the leader is still followed by only one other ant, but the contact between them is by no means so constant and "the second ant does not keep so very close behind its leader; it often falls two or three inches in rear, yet it does not lose its way. Nor is a continuous succession of touches necessary in order to enable it to keep its place. . . . Now, since the instinct has reached that stage of development when tactile communication is no longer required, it might be thought that the second ant follows the first by employing its sense of sight. . . . This certainly is not the case. As the pair advances through the jungle of leaves, it often enters some difficult place. The second ant finds it hard to maintain its position; as a result it falls a few inches in rear while the leader turns in and out amongst the leaves and is lost to the follower's view. But this does not break the connecting link; the second ant follows on the track of the first, even though its leader is out of sight. . . . The primitive tactile communication has been abandoned; it has been replaced by the faculty of smell.

"Let us turn now to a third species, the common black ant, or *Camponotus compressus*, and we will see how this faculty of communication has advanced another stage." The discoverer in this case, enters the nest, " remains inside for a minute or two, and when it emerges we see a troop of workers following closely in its train. . . . The ants, thus formed into a compact party, advance, one close behind the other, often in a single line. . . .

" Here, therefore, we see a further step in the instinct. A single follower has been replaced by a group of workers. It is an advance in degree rather than in kind, for each one in the line follows the one in front by employing its sense of smell. . . .

" Thus, what at first sight seems an act of considerable complexity can be reduced to very simple terms. . . . The stages in the process may be summarized thus. It originated in one ant leading out another and maintaining connection by the very simple process of the second ant repeatedly touching the first. But this, being a tedious mode of progression and liable at any moment to result in a break, was far too inefficient for the requirements of the ants, and must soon have begun to improve. The follower then commenced to use its sense of smell, and, as a consequence, the tactile communication became less important and therefore began to disappear. At the same time the leader ceased to render assistance, since the follower was now able to retain its position by the use of the more subtle sense. Additional workers now began to join in the procession, each following on the one in front under the guidance of its olfactory sense. But still they remained dependent on their leader for conducting them along the right road. As the olfactory faculty continued to improve, their reliance on a leader became proportionately less. Then the followers began to move on their own accord, provided that they were supplied with the line of scent. Their leader was still of some value to them ; they frequently communicated with it to gain reassurance and without it they still often went astray. One further advance in the olfactory sense brought them to the most developed state. They had now reached the condition of the *Pheidole* ants ; the few followers had grown into a multitudinous army which was quite independent of any leader and needed only a momentary contract [sic] with a worker to enable it to follow on the line of its scent. Such I believe to be the origination and the mode of evolution of an instinct which, in its finished complexity, defies our attempts to understand. A tactile communication was its rudimentary beginning; its progress depended on successive refinements in the ordinary sense of smell."

We have quoted rather fully Hingston's interesting observations, without necessarily subscribing to his theory, which seems to us rather too facile, while his use of the terms, "instinct" and "faculty" is decidedly uncritical.

Eidmann has experimented critically on European ants, and described the results in several suggestive papers.* He is especially interested in the question whether ants can not only spread the news that they have found something (*indicative* means of communication), but also tell the nature and position of their find (*descriptive* means of communication). We have seen above that most previous workers denied this latter possibility. But Eidmann shows that, although the phenomena known at present seem all explicable in terms of indicative means of communication, the other cannot yet be definitely ruled out of court. He probably visualizes the possibility of a method analogous to that employed by bees (see Note 55). In his experiments, the food was never found by the helping party of workers when he arranged matters so as firstly, to prevent the finder leading her nest-mates back, and secondly, to destroy all vestiges of her odorous trail. Eidmann does not, however, regard this as conclusive proof, "since the finder, when it gave the alarm, certainly could not know that it would be kidnapped immediately it left the nest, that its tracks would be obliterated, and that it would have to declare exactly where the find was situated."

Curiously enough Eidmann found that when the booty consisted of small pieces which the finder could carry, one by one, without assistance, there was no alarm spread and no help. The finder alone made repeated journeys (in one experiment no fewer than twenty-three) till all was gathered in. Even then it continually revisited the spot, apparently unable to judge whether it was empty.

NOTE 43.—(See also next note and Note 1.) This is not the place to thrash over anew the details of the old

* Eidmann, H., 1925, "Das Mitteilungsvermögen der Ameisen," *Naturwissenschaften*, Berlin, Bd. 13, pp. 126–8. 1927, "Die Sprache der Ameisen," *Rev. zool. Russ.*, Moscow, t. 7, pp. 38–48 (German with Russian summary).

controversy as to whether insects are automata—mere reflex-machines—or conscious beings. It is one of those questions, so frequent in modern biology, which seem destined to be restated rather than to be solved. If Nature refuses our demand for a simple "yes" or "no", the probability is that our question is a foolish one.

With regard to ants, the social conditions under which they live "make it extremely difficult or even impossible to determine to what extent the behaviour of the individual insect is the result of the constantly acting social medium in which they are immersed, and to what extent it depends on inherited mechanisms. This difference is also responsible for the differences in the interpretation of behaviour by different investigators. The physiologist who studies social insects merely as individual organisms, experimentally isolated from their social medium, is apt to conclude that their behaviour is entirely reflex, or tropistic (Bethe, 1898, 1900, 1902, and Henning, 1916), whereas those who observe them in their social environment reach a very different conclusion, and while admitting that many of their activities are reflexes ('automatic' behaviour of Forel) feel confident nevertheless that they give unmistakable evidences of memory, appetites, emotion, imitation, and a feeble intelligence, or ability to modify their reactions in conformity with previous experience and environmental changes ('plastic' behaviour of Forel). General agreement on these matters still leaves plenty of room for differences of interpretation in detail, according to the training, predilections and philosophic outlook of the investigator. Forel and Brun, trained as neurologists, are greatly impressed by organic memory, and make constant use of Semon's 'mneme' and his terminology in describing the behaviour of social insects. The Jesuit father, Wasmann, trained in the scholastic philosophy, operates with 'instincts', virtues and faculties (Vermögen) in the manner of St. Thomas Aquinas, and with the adroitness for special pleading and ignoring of pertinent data for which his order is so celebrated, wraps the whole subject of myrmecology and myrmecophily in a dense fog of teleology, 'Fremddienlichkeit', amical selection, mimicry and theistical casuistry. Within recent years I have come increasingly to avoid the word 'instinct' and to prefer 'appetite', or 'appetition' in Fouillée's sense (Wheeler, 1921*c*). Of course, this is nothing new, since the word was used with much the same signification by the scholastic philosophers (*appetitus sensitivus*, Wasmann's 'sinnliches Begehrungsvermögen'). It is Aristotle's ὄρεξις and is synonymous with the 'libido' and 'craving' of modern psycho-analysts." (Wheeler, 1928, pp. 225–6.)

Forel (1928, i, p. 243) makes an interesting comparison. "We will now assume, at what risk it matters not, that the engrams [memories] acquired during the life of man by study, by books and most of all by well-reasoned and laborious reflection, constitute *on an average* 60 per cent. of his thought and will, and thus also determine 60 per cent. of his actions. I fear, indeed, that this figure may be too high. The rest is due to hereditary dispositions, to constellations of instinctive passions and to the imitative prejudice in favour of the acquired routine followed by the unreflecting majority. We will assume on the other hand that in the ant, instinct fixed once for all by heredity constitutes alone 95 per cent. of the thought, will, and action. To these we may add 4 per cent. due to emotional constellations, and the routine of habits fairly rapidly acquired (secondary automatisms). Even then, 1 per cent. still remains for reflection, which can modify the ant's actions according to circumstances and special cases.

"One per cent., forsooth, is very little; such a trifling fraction can only be perceived by close attention and much perseverance on our part. That is why it is missed by the majority of those human beings who look at ants, and also why this same majority regard insects as mere machines, whereas they consider themselves to be created in the image of God. I really do not think I have exaggerated anything or committed any error in my comparison, summary as it may be."

Note 44.—(See also Notes 1 and 43.) On a basis of mnemic psychology, Forel (1928, i, p. 244) has no difficulty in attributing to ants "flashes of reason". He writes: "Individual memory acquired in the course of life, in other words, the sum of the engrams acquired and combined with each other, and capable of combining with the hereditary instincts, this memory or mneme, I repeat, constitutes the basis of all reasoning in ourselves as in the ants. When an ant instinctively *seeks* or *avoids* something and *discovers* the *object* she has been seeking, or a place of *shelter*, she desires, still instinctively, to inform her companions. But in order to do so, by means of the signs also instinctively inherited in the antennal language, she must not only *find* her way again, but also *lead* her companions thither, either by carrying them or by making signs. It is here that acquired memory comes in. The best proof of this lies in her *doubts, hesitations, and mistakes*, particularly clear in the expeditions of *Polyergus rufescens*, of which we shall speak in Part IV, but also in the above-quoted experiments. She does this by comparing the sudden quandaries in which the experimenter may happen to place her, or even a haphazard situation unforeseen by *instinct*, with the *memories* she has personally acquired of places and of her *companions*. It is then that flashes of reason are produced."

Brun,* with a similar philosophic outlook, credits the higher social Hymenoptera (especially ants) with a considerable power of sensory association and even of forming abstractions and drawing conclusions. He instances Forel's experiment with bees which were fed with honey on artificial flowers of coloured paper. Later were put out pieces of paper with no resemblance to flowers and no honey. The bees searched these too. Brun explains that the bees had acquired the sensory association " honey-taste-coloured paper flowers ", and therefore ransacked all the blooms. But their seeking further on differently-shaped bits of paper shows that they had also formed a sensory abstraction, " paper," and on the basis of this, had drawn a " sensory conclusion by analogy " (*sinnlich Analogieschluss*) " which we can formulate as follows : If honey is found on paper ' flowers ', it may also be present on other scraps of paper ".

Forel and Brun among others insist on a correlation between these higher psychic capacities and the development of the *corpora pedunculata*, or mushroom bodies, of the insect brain. They have been compared with the human cerebrum and have even been described by Forel as " the

* 1920, " Die psychischen Fahigkeiten der Insekten," *Mitt. Entom.*, Zurich, 5, pp. 293–321, 1 pl. 1921, id. *Mitt. Schweiz. Ent. Soc.*, 13, pp. 111–13.

organ of the memory, the social habits and the small reflective capacity possessed" by ants. It is true that these bodies reach their highest development among insects, in the social Hymenoptera and above all in the worker caste of the ants.

Wheeler, however, remarks that the *corpora pedunculata* are even more highly developed in a number of other invertebrates which are by no means noted for intelligence, and above all in the king-crab (*Limulus*) in which * "the corpora pedunculata are so large and complicated that they resemble the cerebral hemispheres of a higher vertebrate! They have, in fact, advanced much further in relative volume and morphological differentiation beyond the ant corpora pedunculata than have the latter beyond those of the lower Orthopteroids. I ask again, therefore, what is such a stupid and archaic creature as Limulus doing with the most highly developed corpora pedunculata in the whole Arthropod phylum? Forel says he knows nothing about Limulus and seems to imply that he cares less, so convinced is he of the precise function of the structures in question, but if they are really an infallible index to the 'plastic-psychical and individual mnemic capacities of insects', as Brun contends, we must assume either that Limulus, somewhere in the depths of the sea and quite unknown to us, exhibits an extraordinary degree of 'plastic mentality', or that its extraordinary corpora pedunculata are a wonderful depository of 'mnemic engrams', perhaps painfully acquired by the enterprising Palæozoic Protolimulus and transmitted as useless heirlooms to its modern moronic descendants!"

NOTE 45.—The following is Lubbock's own note (pp. 407–8 of Appendix G in the seventeenth edition) on this question :—

ON THE FUNCTION OF THE COMPOUND EYES AND OCELLI

Forel agrees with Réaumur, Marcel de Serres, and Dugès, that in insects which possess both ocelli and compound eyes the ocelli may be covered over without materially affecting the movements of the animals; while, on the contrary, if the compound eyes are so treated, they behave just as in the dark. For instance, Forel varnished over the compound eyes of some flies (*Calliphora vomitoria* and *Lucilia cæsar*), and found that if placed on the ground they made no attempt to

* Wheeler, 1928, p. 178, foot-note.

rise, while if thrown in the air they flew first in one direction and then in another, striking against any object that came in their way, and being apparently quite unable to guide themselves. They flew repeatedly against a wall, falling to the ground, and unable to alight against it, as they do so cleverly when they have their eyes to guide them. Finally, they ended in flying away straight up into the air and quite out of sight.

Johannes Müller inclined to the opinion that insects saw near objects with their ocelli. Plateau satisfied himself that the movements of insects are not affected by the ocelli being covered over, and hence concluded that they are rudimentary organs. The complexity of their structure, however, seems fatal to this conclusion.

Forel confesses that the use of the ocelli still remains an enigma, but he is disposed to think that they enable their possessors to see in comparative darkness. He observes * that they are specially developed in insects which require to see both in bright light and also in comparative obscurity. Aërial insects do not generally require or possess ocelli.

Lebert expresses the opinion † that in spiders some of their eight eyes—those which are most convex and brightly coloured—serve to see during daylight ; the others, flatter and colourless, during the dusk. Pavesi has observed,‡ that while the species of *Nesticus* possess normally eight eyes, in a cave-dwelling species (*Nesticus speluncarum*) there are four only, the four middle eyes being atrophied. This suggests that the four central eyes serve specially in daylight.

NOTE 46.—It is impossible to explain satisfactorily the mode of vision of compound eyes without the aid of figures and diagrams. Suffice it to state here that in its essential features, Müller's mosaic theory (1826) still holds the field. The most important modifications have been due to the work of Exner.§ An interesting account of butterfly vision, with some remarkable illustrations, has been contributed

* L.c., p. 181.

† *Die Spinnen der Schweiz*, p. 6.

‡ "Sopra una nuova specie di Ragni appartenente alle collezioni del Museo Civico di Genova," *Ann. Mus. Civ.*, 1873, p. 344.

§ 1891, *Die Physiologie der Fazettierten Augen von Krebsen und Insekten*, Wien.

by Eltringham,* and should be consulted by those interested.

A very important feature in insect vision is the immobility of the eyes. As there can be no focussing, it seems certain that perception of forms more than a few feet away is very indistinct. Movements, however, can be perceived at greater distances, and abrupt movements, suddenly affecting a series of ommatidia in succession, are especially noticed (Imms).

Eltringham is impressed with the imperfections of the compound eye as an organ of vision. After describing the vertebrate eye, he writes: "When, however, we come to the eye of an insect we find that nature in a wanton mood has evolved an apparatus of infinitely greater complexity, but of probably inferior performance. . . . For its size the butterfly's eye is, at close quarters, perhaps the most efficient type of the compound eye, and yet the insect is very short-sighted and probably unable to recognize even another of its own kind at a distance of more than three or four feet."

This spring I made an observation which seems to corroborate this shortsightedness. A much worn, male small tortoiseshell butterfly (*Vanessa urticæ*) was chasing persistently a queen wasp (*Vespa*, probably *V. germanica*). The latter doubled and twisted, and the butterfly followed every turn extremely closely—often only an inch or two behind. The pursuit was accompanied by a loud rustling like that of some Acridiids when flying. This rustling, apparently made by the butterfly, though I could not be sure, ceased when I disturbed the chase; the insects circled round separately; the butterfly was netted but the wasp escaped.

NOTE 47.—The following is Lubbock's own note (pp. 403–7 of Appendix G in the seventeenth edition) on this question:—

On the Colour-sense of Ants

Professor Graber † has published an interesting memoir on this subject. He confirms the observations on ants and

* 1919, Butterfly vision, *Trans. Ent. Soc. London* (1919), pp. 1–49, pls. 1–5. There is a more popular description by the same author in his book, *Butterfly Lore*, Oxford, 1923, pp. 117–28.

† "Fundamental-Versuche über die Helligkeits- und Farben-Empfindlichkeit augenloser und geblendeter Thiere," *Sitz. Kais. Akad. der Wiss.*, Wien, 1883.

Daphnias, in which I showed that they are sensitive to the ultra-violet rays, by similar observations on earthworms, newts, etc. It is interesting, moreover, that the species examined by him showed themselves, like the ants, especially sensitive to the blue, violet, and ultra-violet rays. Professor Graber, however, states that he differs from me, inasmuch as I attributed the sensitiveness to the ultra-violet rays exclusively to vision; that it is "ausschliesslich durch die Augen vermittelt". I would not, however, express that opinion as applying absolutely to all animals, though it is, I believe, true of ants, where the opacity of the chitine renders it unlikely that the light would be perceived except by the medium of the eyes and ocelli.

Graber has demonstrated in earthworms and newts, and Plateau in certain Myriapods,* that these animals perceive the difference between light and darkness by the general surface of the skin. But, more than this, Graber appears to have demonstrated that earthworms and newts distinguish not only between light of different intensities, but also between rays of different wave-lengths, preferring red to blue or green, and green to blue. He found, moreover, as I did, that they are sensitive to the ultra-violet rays. Earthworms, of course, have no eyes; but thinking that the light might perhaps act directly on the cephalic ganglia, Graber decapitated a certain number, and found that the light still acted on them in the same manner, though the differences were not so marked. He also covered over the eyes of newts, and found that the same held good with them. Hence he concludes that the general surface of the skin is sensitive to light.

These results are certainly curious and interesting; but, even if we admit the absolute correctness of his deductions, I do not see that they are in opposition to those at which I had arrived. My main conclusions were that ants, Daphnias, etc., were able to perceive light of different wave-lengths, and that their eyes were sensitive to the ultra-violet rays much beyond our limits of vision. His observations do not in any way controvert these deductions: indeed the argument by which (p. 234) he endeavours to prove that the effect is due to a true light and not to warmth, presupposes that sensations which can be felt by the general surface of the

* *Journ. de l'Anatomie et de la Physiologie*, 1886, p. 431.

skin are still more vividly perceived by the special organs of vision.

Professor Graber's observations have been followed up by M. Forel.* He took fifteen specimens of *Camponotus ligniperdus*, which is a large species, and, moreover, possesses the advantage, for this purpose, of having no ocelli, and carefully covered the eyes with opaque varnish. He then placed them in a box with ten normal specimens of the same species (to which he subsequently added five more), and covered over one half of the box with cardboard and the other half with a layer of water. In this way the one half of the box was darker than the other, but the temperature of the two sides was approximately equal. In four experiments the numbers were as follows :—

Under the Cardboard.		Under the Water.	
Hoodwinked Ants.	Normal Ants.	Hoodwinked Ants.	Normal Ants.
3	9	12	1
13	7	3	3
9	9	5	1
3	8	12	2
—	—	—	—
28	33	32	7

It will be seen that a very large majority of the normal ants in every case went under the cardboard ; while it was practically indifferent to the hoodwinked ants in which side of the box they rested. Moreover, every time the water and the cardboard were transposed, the normal ants were much excited and began running about to avoid the light, while the hoodwinked ants were quite unaffected.

These experiences, therefore, proved that the varnish did, in fact, render the ants temporarily blind, their instincts being in other respects unaffected.

He then replaced the cardboard and water by a solution of esculine, which is impervious to the ultra-violet rays, and a glass of deep cobalt, which stopped most of the other rays but permitted the ultra-violet to pass. The results then were :

* Rec. Zool. Suisse, 1887.

Under the Esculine.		Under the Cobalt Glass.	
Hoodwinked Ants.	Normal Ants.	Hoodwinked Ants.	Normal Ants.
11	8	3	1
11	13	4	2
9	12	5	3
5	13	9	2
10	12	4	3
3	11	12	3
12	13	3	1
61	82	40	15

Thus, then, a very large proportion of the normal ants preferred to avoid the ultra-violet rays by going under the esculine. To the varnished ants, on the contrary, it was indifferent whether they were under the esculine or the cobalt. The slight preponderance in favour of the esculine was probably partly due to having started the experiments with a larger number of ants in the side of the box then covered with esculine, and partly from the fact that the hoodwinked ants would have a tendency to accompany the others.

From these and other experiments, M. Forel comes to the same conclusion as I did, that the ants perceive the ultra-violet rays with their eyes ; and not, as suggested by Graber, by the skin generally.

Experiments with *Platyarthrus*

In connection with this subject I may add that I do not at all doubt the sensitiveness to light of eyeless animals. In experimenting on this subject I have always found that though the *Platyarthrus*, which live with the ants, have no eyes, yet if part of the nest be uncovered and part kept dark, they soon find their way into the shaded part. It is, however, easy to imagine that in unpigmented animals, whose skins are more or less semi-transparent, the light might act directly on the nervous system, even though it could not produce anything which could be called vision.

[Editor's Note.—Curiously enough, Eidmann and Escherich have shown that *Platyarthrus*, despite its blindness, regularly accompanies its hosts (*Lasius*) to the herds of " milch-cows " (aphides) when these are visited, on bushes at considerable distances from the nests, for purposes of milking. But these milking excursions, at least in summer, when *Platyarthrus* is observed on them, take place chiefly about midnight. If *Lasius flavus* (and presumably *Platyarthrus*) visit the herds by daylight, it does so by means of tunnels through the soil. The part taken by this little blind wood-louse is not known.

NOTE 48.—It seems very probable that the " ants " which Colonel Long saw " seduced " from their holes by the songs of maidens, were not really ants, but termites (the so-called " white ants "), which we know to be used for food by many primitive peoples. Thus Mr E. Evans-Pritchard informs me that the Azande of the Sudan are accustomed to gather termites in large numbers for food by tapping the termitaria with sticks in a ritual manner, to cause a flight of the winged forms. Similarly Boyes * says that in the Congo " the white ant, . . . is looked upon as a great delicacy, and is eaten roasted in much the same way as locusts are eaten by certain tribes in South Africa. About the beginning of the rainy season, when the white ants get their wings, the Natives enclose the nests with huge basket-work frames, and two Natives take their posts at each ant-heap One of them proceeds to beat the ground around the nest, with two sticks, producing a drumming sound similar to that caused by the fall of a tropical rainstorm, while the other, from time to time, pours a little water down the entrance to the nest. This completes the illusion, and the ants, thinking that the rainy season has at last arrived, come out in their thousands, only to be gathered up and roasted by the ingenious natives. It appears that this practice is not confined to the Congo, but is also in use in Uganda and in parts of Tanganyika Territory, where the Natives look upon roast white ants as a desirable and appetising luxury."

Hegh † gives a detailed account of the Congo procedure, which is definitely used for termites. " The negro captures termites at any time by thrusting in at the foot of the mound a pointed stake six feet long (1 m. 75) ; when the hole reaches the depth of a yard (1m.), he places in it a little broom made of grass roots (masele). He then leans over the opening and

* " The Company of Adventurers," *East Africa*, 1928, p. 41.
† *Les Termites, Partie generale*, Bruxelles, p. 676.

makes with his tongue a special noise, imitating, according to him, falling rain. He turns the broom gently, the termites hook on to it; he draws them out, eats them one by one or throws them into a bucket of water."

The observations of Boyes and of Evans-Pritchard seem to indicate that the termites are taken chiefly at swarming-time, when clouds of the winged sexual forms leave the nest, and the emergence of the swarm is merely accelerated by songs and tapping. Most of Hegh's Congo correspondents also state that it is at swarming-time that the natives await the termite-crop. Only the one we have quoted above, who, on the contrary, expressly describes termite-catching to take place at any time, mentions a procedure of enticement, and in this case it apparently attracts the wingless forms (workers, etc.). One correspondent, however, seems with Boyes and Evans-Pritchard, to stress the ceremonial nature of the termite-catching. "At the period of swarming, I have noticed that the Balubas come together, singing traditional songs and thus drawing the attention of the inhabitants to the harvest about to be gathered in. In the same way I have remarked that the work of catching the termites is accompanied by songs."

It is obvious that an explanation of the above phenomena demands experimental work. One is tempted to suggest that the usual time of swarming is the beginning of the rainy season—or even more precisely, that the effective stimulus for actual emergence is the first shower after the dry season, and that a sound like that of rain exerts the same effect. Fortunately there is independent evidence as to the swarming period. Thus Hegh (op. cit., p. 145) writes that: "the period at which swarming occurs varies according to the climate and to the species. It depends on the time when the winged caste reaches full maturity and becomes able to fly. Often, in the tropics, this event, important in termite-life, coincides with the beginning of the rainy season." This is especially so in the Congo. We should have yet, however, to explain the attraction exercised, according to one correspondent, at other seasons.

NOTE 49.—It has often been supposed that the ants are descended from a Mutillid-like ancestor. Even such a high authority as Emery subscribed to this view, which is rendered very unlikely by the fact that female Mutillids are entirely wingless, while queen ants are, of course, fully winged. It is therefore reasonable to suppose that the ancestors of ants were also winged in both sexes. For a detailed discussion of the origin of ants, based on a wide range of morphological and palæontological data, the interested reader should consult Wheeler (1928, Lecture 5), who considers that "the group which deserves the most serious attention in connection with the ancestry of ants is the Tiphiidæ and especially the genus Elis (*Myzine*) since it resembles the ants in the shape of the eyes, the wing-venation and the generalized tendency to constrictions between all the abdominal segments, so reminiscent of certain" very primitive ants.

NOTE 50.—Forel, of course, has long lent the heavy weight of his authority, as entomologist and psychologist, to the opinion that not only ants, but insects in general, are deaf. It is true that many experiments clearly indicate in insects an entire unconcer with vibrations which seem very loud noises to us; it is probable also that their very small size and the nature of their framework—a rigid exoskeleton—makes them sensitive to vibrations, imperceptible to us, which they perceive by other means than hearing in the strict sense of the term. There is, however, as we shall see, considerable experimental evidence that insects can hear, and there are in very many insects, on the one hand complicated structures devoted exclusively to the production of special sounds, and on the other hand, exceedingly complex organs to which it is difficult to assign any other function than that of hearing. The most remarkable of the latter are those now called chordotonal organs, first found by von Siebold in the front legs of Orthoptera, later described by Lubbock in certain ants, and known to-day in a number of other groups. Perhaps the most highly specialized of all is that recently described by Vogel in cicadas.

Forel's view, since it involves a special criticism of Lubbock's work, may be quoted rather fully. He does not consider it proven that the chordotonal organs are hearing organs, nor that they can function in any way analogous to that of the human ear. He writes (1928, i, p. 216) that "apart from crickets, some locusts and grasshoppers, the other insects always appear to remain deaf as soon as we eliminate the mechanical shocks to which all of them are highly sensitive. Lubbock even tried to produce sounds too high to be heard by the human ear. He succeeded, but no insect reacted to them, and he was obliged in the end to adopt the view shared by Huber, Perris, and myself, namely, that hearing cannot be proved in bees, wasps, and ants. In spite of this, he persisted in believing that insects hear sounds which we do not hear. I have myself scraped the high strings of a violin an inch or so away from some bees which were foraging in the flowers. I have shouted and whistled with all the force of my lungs equally close to various insects, while protecting them from my breath. So long as they did not see me, they paid no attention. We can hardly give much credence to Léon Dufour, who thought that he had proved hearing in crickets—because they ceased their chirping when he struck the ground with his foot two or three yards away from them, and in *Annobium* [sic] (furniture beetles) because they are silent when a chair is moved. He forgot that the deaf and dumb feel the rumbling of a carriage at a distance.

"Sound-waves, especially those of low-pitched sounds, bear a much closer resemblance to powerful mechanical shocks than luminous, caloric or electric waves. Hearing has therefore a fundamental connection with touch, but we human beings make a clear distinction between the perception of a very low sound by touch and the audition of the same sound. We must not forget that man's sense of hearing, having its energy specialized in one organ, has attained to a nicety of detail that has no equal even among the lower vertebrates. This, I consider, is the sense which separates us most widely from the insects and lower animals. When we come to fishes, the acoustic nerve is confused with other nerves, and the cochlea, that portion of the inner ear which in ourselves is more especially affected in audition, has disappeared."

"Miss Fielde produced vibrations on all kinds of instruments—as many as 60,000 vibrations per second—in front of the artificial nests of various species of ants, without obtaining the least reaction. Will, on the other hand, makes incidental mention of an experiment he made on the beetle *Cerambyx Scopuli*. He enclosed a female in a box, and claimed that every time he irritated her with a pin fixed in the wall of the box and caused her to stridulate, the male which he had placed about 6 inches away would hear her and grow restless and move towards the box. He thinks that insects hear only the stridulations of their own species. By way of contrast to this experiment, I must mention those of Perris, who 'made Diptera buzz and scraped the corselets of Longicorns, etc.,' some distance away from individuals of the same species, but of different sex, and could elicit no particular response.

"All these facts, so it seems to me, combine to show that if insects, particularly ants, have any hearing, it takes place in *some way different from our own*, even in crickets and locusts. We are justified in assuming that they perceive the stridulations of their own species as shocks at a certain distance, but in a manner we cannot yet understand very well; nothing more can be said at present.

"Wheeler considers that stridulation in the *Myrmicinæ*, *Ponerinæ*, and *Dorylinæ* is an important means of communication ignored by many authors. Turner found that *Formica* respond to vibrations by rushing outside in an excited fashion. Turner thought that in his experiments he had adequately eliminated the possibility of mechanical concussion from the foundation on which his ants were resting. Wheeler thinks that ants perceive stridulations through the air by their chordotonal organs. Miss Fielde and I remained sceptics in this respect, though we did not deny the results of the experiments made by Wheeler and Turner. I do not deny a certain kind of hearing in ants, but I do not think that their audition is the same as ours; it is, I repeat, quite another thing."

Wheeler, on the other hand, is strongly inclined to believe that ants hear, in the sense of perceiving aerial vibrations. He writes that "stridulation, at least among the Myrmicinæ, Ponerinæ, and Dorylinæ, is an important means of communication, which Bethe has completely ignored and even Forel and other myrmecologists have failed to appreciate. It readily explains the rapid congregation of ants (Myrmicinæ) on any particle of food which one of their number may have found, for the excitement of finding food almost invariably causes an ant to stridulate and thus attract other ants in the vicinity. It also explains the rapid spread of a desire to defend the colony when the nest is disturbed. This is especially noticeable in species of *Pheidole*, *Myrmica*, and *Pogonomyrmex*. It is the secret of being able in a short time to catch ants like *P. molefaciens* in great numbers by simply burying a wide-mouthed bottle up to its neck in the mound of the nest. An ant approaches and falls into the bottle. It endeavours to get out, and failing, begins to stridulate. This at once attracts other ants which hurry over the rim and forthwith swell the stridulatory chorus till it is audible even to the human ear. More ants are attracted and soon the bottle is filled. If it be corked and shaken for the purpose of still further exciting its contents, and then held over another *Pogonomyrmex* colony whose members are peacefully sauntering about on the dome of the nest, the wildest excitement will suddenly prevail, as if there had been a call to arms—or to dinner. Even more remarkable is the stridulation in a colony of *Atta fervens* (= *texana*), the Texan leaf-cutting ant. Here the different ants, from the huge females through the males, large soldiers and diminishing castes of workers to the tiny minims, present a sliding scale of audibility. The rasping stridulation of the queen can be heard when the insect is held a foot or more from the ear. To be audible the male and soldier must be held somewhat closer, the largest workers still closer, whereas the smallest workers and minims, though stridulating, as may be seen from the movements of the gaster on the post-petiole, are quite inaudible to the human ear. It is not at all improbable that all this differentiation in pitch, correlated as it is with a differentiation in the size and functions of the various members of the colony, is a very important factor in the coöperation of these insects and of ants in general. The contact-odor sense, important as it undoubtedly is, must obviously have its limitations in the dark, subterranean cavities in which the ants spend so much of their time, especially when the nests are very extensive like those of *Atta*. Under such conditions stridulation and hearing must be of great service in maintaining the integrity of the colony and of its excavations." (1910, pp. 513–14.)

Commenting later on this, Wheeler remarks (1910, p. 514) that " If the view of Miss Fielde and Parker be accepted, we must suppose that the *Pogonomyrmex* in the experiment above described, were thrown into agitation by vibrations passing from the bottle of stridulating ants through my body to the soil of the nest. It seems to me much more probable that the ants perceived the stridulation directly as aërial vibrations ". After describing more detailed experiments by Turner, Wheeler admits that it is extremely difficult to exclude the possibility of vibrations in the substratum—felt rather than heard—and quotes Miss Fielde and Parker that it may be " misleading to attempt to distinguish touch from hearing, and we shall be more within the bounds of accuracy if we discuss the question from the standpoint of mechanical stimulation rather than attempt to set up questionable distinctions based upon human sensations ".

Snodgrass (1926) and Eggers (1923) * range themselves with those who consider that the chordotonal organs are primarily not organs of hearing. " Concerning the function of the chordotonal organs nothing definite can be said. In the text books the chordotonal organs are presented as ' organs of hearing '. It is certain, however, that the perception of sound has not been proved to be connected with any of them, and those organs situated within the legs, the wing bases, and various regions of the body where they are affixed to solid parts of the body wall, even though they may be associated with enlarged tracheæ, seem poorly adapted for acoustic purposes. On the other hand, the internal position of the organs suggests that they must have some function connected with the workings of internal parts of the body. Following this idea, the discussion of Eggers (1923) on the possible uses of the chordotonal organs leads to conclusions more convincing than any other yet presented bearing on the function of these enigmatical structures peculiar to insects.

" Eggers points out that most of the movements made by insects result in rhythms. Especially is this true of the wing mechanism, which sets the whole body into rapid vibration ; but also the motions of the antennæ and the legs tend to become rhythmical, while the movements of

* Snodgrass, R. E., 1926. " The Morphology of Insect Sense Organs and the Sensory Nervous System," *Smithsonian Misc. Coll.*, vol. lxxvii, No. 8, 80 pp., 32 figs.

Eggers, F., 1923. " Ergebnisse von Untersuchungen am Johnstonchen Organ der Insekten und ihre Bedeutung für die allgemeine Beurteilung der stiftführenden Sinnesorgane," *Zool. Anz.*, Bd. 57, S. 224–40, 2 figs.

respiration, the pulsations of the heart, the bodily motions of locomotion in certain aquatic larvæ are all of a rhythmic nature. Since rhythm, then, is such a characteristic feature of muscular activity in insects, it would seem that there should be special organs for registering it and for regulating the action of the muscles that produce it. The chordotonal organs suggest themselves at once as organs adapted for this purpose, and as the only organs that could serve in such a capacity. According to this idea, therefore, the chordotonal organs are to be regarded as rhythmometers.

"Finally, it is conceivable, as suggested by Eggers, that if a chordotonal organ is connected with a thin membrane of the body wall, or is sufficiently delicate in its construction, it might be responsive to motions of the surrounding medium ; i.e. to vibrations of air or water, and hence might act as a receptor of sound waves. Thus, for example, the highly developed organ of Johnston in the antenna of the Culicidæ (fig. 31B) or the tympanal organs of the Orthoptera may be organs of hearing." (Snodgrass, l.c., p. 64.)

We have elsewhere * gathered together the evidence that cicidas can hear, but that it is a specialized hearing, adapted chiefly to perceive the song of the species concerned, and sounds of a similar kind. It also seems to us that the work of Regen † on Orthoptera has not received the attention it deserves. This author, by the most ingenious and controlled employment of phonograph records of field-cricket song, and of males enclosed in various ways with females in which the chordotonal organ had been extirpated in the last pre-adult stage, and with females possessed of all their powers, prove conclusively that the song serves to attract and to orientate the female towards the male.

NOTE 51.—The following is Lubbock's own note (pp. 408–10 of Appendix G in the seventeenth edition) on this question :—

SENSE OF SMELL

In my previous memoirs I have recorded a few experiments which convinced me that ants are gifted with a very

* Myers, J. G. and Myers, I. H., 1928. The significance of cicada song. *Psyche*, London, No. 32, pp. 40–57, 5 figs.

† Regen, J., 1912. "Experimentelle Untersuchungen über das Gehör von *Liogryllus campestris* L., *Zool. Anz.*, Bd. 40, pp. 305–16, and other papers.

highly developed sense of smell, and that this resides in the antennæ. Forel, Graber, Lefebvre, Perris, and other recent writers have come to the same conclusion, and there can, I think, be no reasonable doubt that in very many insects the antennæ serve as organs of smell. At the same time it does not necessarily follow that the sense of smell should be confined to them. Even in ourselves it is not always easy to distinguish the sense of taste from that of smell.

Graber deprived a beetle (*Silpha thoracica*) of its antennæ, and then tested it with oil of rosemary and asafœtida. A beetle of the same species, but with antennæ, showed its perception by movement in half a second to one second in the case of the oil of rosemary, and rather longer, one second to two seconds, in the case of the asafœtida. The *Silpha* without antennæ showed its perception of the oil of rosemary in three seconds on an average of eleven times, while in no case did it show any indication of perceiving the asafœtida even in sixty seconds.

Professor Graber infers, " dass der eine Geruchsstoff (Assafœt), der nichts weniger als ein sehr feiner ist, nur durch das Medium der Fühler perzipiert Bewegungen auslöst, während der andere (Rosmarinöl) ähnliches auch ohne Vermittlung dieser angeblich spezifischen Geruchsorgane bewirkt."

Graber questions some of the experiments which seemed to me to demonstrate the existence of a sense of smell in ants. He says :—

" Da Lubbock noch hinzufügt, dass keiner, der das Benehmen der Ameisen unter diesen Umständen beobachten würde, den geringsten Zweifel an ihrem Geruchsvermögen haben könnte, wählte ich auch diese Methode, um zu erforschen, wie sich etwa der Fühler beraubte Ameisen verhalten würden. Ich war nicht wenig überrascht zu finden, dass auch diese (es handelt sich um *Formica rufa*) vor dem Riechobjekt umkehrten. Um ganz sicher zu gehen, versuchte ich's aber noch mit dem gleichen Arrangement aber *mit Weglassung des Riech*-Stoffes, und siehe da ! sie kehrten auch jetzt noch um ! Bei genauerer Beobachtung der von einer Ameise vom Anfang an auf dem Papiersteg zurückgelegten Strecke stellte sich auch bald heraus, dass es sich bei dem gewissen Umkehren lediglich um ein versuchsweises Abschrieten oder Ausprobiren des unbekannten Weges handelt, oder das sich die Ameisen ähnlich benehmen wie wir selbst, wenn wir etwa auf einem schwanken Brette eine tiefe Gebirgskluft überschreiten sollen." *

M. Graber's observation is, I doubt not, quite correct, but his inference is not well founded, nor was his experiment the same as mine. It is quite true that if an ant be started off along a narrow paper bridge, she will after a while turn round and come back again. I do not, however, think that this is due, as he suggests, to any sense of giddiness. Ants which habitually climb trees are not likely to be affected by any such sensation. It is rather, I believe, that they feel they are being sent on a fool's errand. Why should they start off and run straight forward into a strange country? They turn round in hopes of finding their way home, whether the bridge is high or low, broad or narrow, or indeed whether they are on any bridge at all. M. Graber has not observed that I expressly stated that in each case they stopped exactly when they came to the scented pencil.

Editor's Note.—The above controversy between Graber and Lubbock reminds us that the differentiation of the chemical senses in insects is still a problem. The conflicting theories at present in the field have just been reviewed, very lucidly, by Wheeler (1928, p. 239), whom we accordingly quote, but whose book should be consulted for a complete and erudite discussion with references to the literature. Wheeler writes: "that there is abundant justification for taking a different view of taste and smell in insects from that commonly held in regard to these senses in human and mammalian physiology. In mammals the gustatory and olfactory receptors are clearly separate in structure and position, though we are all familiar with the fact that olfaction enters very largely into what we call our taste sensations, and it is known that in certain fishes the taste-buds are scattered over the surface of the body.† In both receptors the nerve terminations are affected by chemical substances dissolved in a liquid or mucous layer overlying them. It is usual to transfer our notions of distinct taste and smell receptors to insects although even in vertebrates taste is not a unitary chemical sense and in insects cannot be distinguished

* V. Graber, "Vergl. Grundversuche über die Wirk. und d. Aufnahmestellen chem. Reize bei den Thieren," *Biol. Centralblatt*, vol. xiii, p. 449 (1885–6).

† Wheeler here adds a foot-note on taste-buds in fishes.

from smell by the structure of the sensillæ.* We have merely acquired the habit of regarding chemoreceptors (sensillæ) on the mouth parts as gustatory and those on the antennæ as olfactory. But lately Minnich (1921, 1922a, 1922b, 1924, 1926) has demonstrated by carefully conducted experiments that butterflies and Muscids taste with their feet (with the four terminal tarsal and distal portion of the basitarsal joints of the second and third pairs of legs). This form of chemoreception is probably of more general occurrence among insects and other Arthropods. Even the distinction between distance receptors for smell and contact receptors for taste does not help us, since insects use their antennæ in both ways as well as for tactile sensations.

"The study of the chemoreceptors of insects leaves us confused and baffled with the variety of the sensillæ and their wide distribution over the body. And the confusion is increased by the difference of opinion in regard to their structure, which grades all the way from sensillæ which may be either tactile or olfactory, through a great variety of presumably olfactory and gustatory to the Hicksian or campaniform sensillæ which have been variously interpreted as organs of pressure, temperature, humidity, or vibration. While most authors believe that the olfactory sensillæ are confined largely or exclusively to the antennæ, McIndoo (1914a, 1914b, 1914c, 1915, 1916, 1917, 1918, 1920), for some inscrutable reason, finds olfactory organs on nearly all parts of the body, except the antennæ, and believes he has secured experimental evidence in support of his contentions. Berlese (1909) in a remarkably lucid account of the olfactory sensillæ, describes them as always containing glandular in addition to sensory cellular elements. He calls attention to the earlier papers of Erichson (1847) and Saulcy (1891), who found the antennæ of insects to be covered with a thin film of liquid. According to Berlese, this film is the secretion of the glandular elements and forms with the olfactory substance a solution which acts on the terminations of the sense cells. It is, indeed, difficult to conceive how olfaction can occur without such a solvent. But other investigators (Hauser (1880), vom Rath (1894), Röhler (1905), Vogel (1911), Hochreuter (1912),

* A foot-note is added here to quote Parker and Öhrwall on gustation in the vertebrates.

Deegener (1912), Demoll (1917), McIndoo, etc.) interpret Berlese's glandular elements as sense-cells and say very little or nothing about an olfactory liquid or its source. . . .

"In certain respects the physiological accounts are more satisfactory than the morphological and leave little doubt that the chemoreceptors are widely distributed over the antennæ, mouth-parts, feet, and possibly other portions of the integument, and that responses to chemical substances either from a distance or on contact are far and away the most important sensory reactions of insects. This is notably true of the social species, and numerous investigators have shown that much of their behaviour is determined by such reactions. . . .

"There is no doubt that the glandular secretions of social insects are emitted in greater volume at times of excitement, but since even the persisting individual, caste, colony, and nest odours are important means of recognition and communication, there is no reason why the odours should not be included with the gustatory stimuli as trophallactic." (See Note 5.)

Wheeler concludes that "the question as to whether an ant or bee smells or tastes its food, a larva, pupa or another ant or bee with its antennæ, is largely academic, or at any rate of no very great physiological significance. Since the words 'taste' and 'smell' are charged with anthropomorphism and the stimuli in both cases are chemical it would be better to use the word 'chemorecept'. And since, moreover, the food stimuli are necessarily chemical, I can see no reason to change the term 'trophallaxis' because it happens that much of the behaviour of social insects is what we have been calling 'olfactory'."

One of the most interesting contributions to the discussion of olfaction in ants is Forel's theory of a "contact-odour sense". His experiments led him "to recognize that the ant's sense of smell must be *different* from ours . . . the antennæ of insects are an olfactory organ turned outwards, protruding into space, and furthermore, very mobile. This certainly allows us to suppose that their sense of smell is much more relational than ours, that it gives them ideas of space and direction, and that for this very reason it is qualitatively different.

"Let us make an assumption—perhaps a very daring one—that the olfactory bulb and the nasal mucous membrane of vertebrates are the result of an invagination of the antennæ and the antennary ganglia of the invertebrate. The nerve terminations which originally protruded are sunk into a cavity, to which they form a lining, and which is placed in communication with the tracheal organ of respiration, so that a current of air, which is continually being renewed, brings odours to them. I for my part believe that this is what has happened. If so, the antennary ganglion has become the olfactory bulb of man and the higher animals, its nerve terminations are numerous small olfactory nerves, and the cerebral antennary lobe has become the olfactory lobe of our brain.*

"As we have just seen, their sense of smell enables the ants not only to perceive odours at a distance, as we and the night-moths can, but to feel them in close proximity and even directly, which we are incapable of doing. It is this which I have described as smell by *contact or topochemical smell.* Since the ants are thus able to feel with their antennæ, which are very mobile in all directions, the smells of all the objects in front, to the right and left, and even behind when they turn round, as they frequently do, they not only obtain a representation of the chemical qualities they have smelt and felt . . . but they can ecphorize † them, and recall them at any moment, as well as their forms in space and their sequence in time, which we cannot do with *our smells.* Thus they are able *to recall smells as round, square, elongated, hard, soft, etc., and as having a certain height and being in a certain direction.*"

Note 52.—One of the latest contributions to the discussion on ants throwing their spoils instead of carrying them is that of Madame Combes.‡ This experimenter suspended a platform some distance above the ground by three strings, scattered on it grains of sugar and scraps of cake (*gaufrette*),

* It is only fair to add that Forel's rather doubtful homologies do not affect the validity of his physiological theory of a contact-odour sense.

† "Ecphorize," in the terminology of Semon's Mnemic theory = "remember".—Ed.

‡ Combes, M., 1925. "Les fourmis jettent-elles les objets volontairement ?" *Ann. Sci. Nat.* (*Zool.*), Paris, (10) 8, pp. 295–300, 2 figs.

and connected it with the ground by two sloping boards. A nest of the wood-ant, *Formica rufa*, was near.

The ants soon found the food and began to carry it off by three different methods. Most of them marched off with it down the sloping boards ; others jumped off the platform with the sugar they had picked up ; finally others, still, threw the sugar or the bits of cake from the platform to the ground.

The platform was then raised considerably. Fewer ants found their way to it, but these still used the three methods of transport (see table below). In the third experiment, the platform was raised more still, only one board was left to connect it with the ground, and this was inclined in the opposite direction, so as to form an overhanging slope for the ants to negotiate.

The results of these three experiments, vouched for by a number of observers, were as follows :—

In the first	44 scraps were carried down the slope ;
with	12 the ants jumped off to the ground ;
	18 were thrown from the platform.
In the second	14 scraps were carried down the slope ;
with	10 the ants jumped off to the ground ;
	2 were thrown from the platform.
In the third	25 scraps were carried down the slope ;
with	66 the ants jumped off to the ground ;
	22 were thrown from the platform.

Lubbock's experiment failed possibly because he used another species of ant—*Lasius niger*.

Madame Combes states that she was able to observe " from very near, and more than once, the movements of the ant carrying its morsel towards the edge and pushing it till it fell, or else dropping it deliberately into space, and I could not, at the moment, doubt the ants' intention of throwing it on the ground. . . . Many ants were marked during the course of the observations, and their faithfulness in pursuing the work made one think that it is in general the same individuals which modify the method of transport according to the conditions."

NOTE 53.—(See also Note 54.) Brun (1920) especially has stressed the fact that distant orientation involves plastic behaviour of a high order—or what some observers would term general intelligence (see Notes 1 and 44). He writes of purely plastic interludes, based entirely on individual memory, and inserted, as it were, between series of automatic, instinctive actions. In the first line among these " intermezzi " come the phenomena of homing, which " constitute a wonderful performance of the small insect brain ".

NOTE 54.—The following is Lubbock's own note (pp. 410–11 of Appendix G in the seventeenth edition) on this question :—

SENSE OF DIRECTION

Fabre has made a number of experiments from which he concludes that Bees have a certain sense of direction. My own experiments led me to a different opinion. I have now repeated some of them, and made others on ants, which all led to the same conclusion. For instance, I put down some honey on a piece of glass, close to a nest of *Lasius niger*, and when the ants were feeding I placed it quietly on the middle of a board 1 foot square and 18 inches from the nest. I did this with thirteen ants, and marked the points at which they left the board. Five of them did so on the half of the board nearest to the nest, and eight on that turned away from it ; I then timed three of them. They all found the nest eventually, but it took them ten, twelve, and twenty minutes respectively. Again, I took forty ants which were feeding on some honey, and put them down on a gravel path about 50 yards from the nest, and in the middle of a square 18 inches in diameter, which I marked out on the path by straws. They wandered about with every appearance of having lost themselves, and crossed the boundary in all directions. I marked down where they left the square, and then took them near the nest, which they joyfully entered. Two of them, however, we watched for an hour. They meandered about, and at the end of the time one was about 2 feet from where she started, but scarcely any nearer home ; the other about 6 feet away, and nearly as much further from home.

I prepared a corresponding square on paper, and, having indicated by the arrow the direction of the nest, I marked down the spot where each ant passed the boundary. They crossed it in all directions ; and if the square were divided into two halves, one towards the nest and one away from it, the number in each was almost exactly the same.

Editor's Note.—The study of distant orientation and place recognition has progressed very greatly since Lubbock wrote. So far as the ants are concerned, however, his results have been very largely confirmed. The literature on the subject, even relating to ants alone, is far too voluminous to cite here, but English readers will find a useful summary, with all necessary references, in the recent work of Rabaud.*

So far as the flying Hymenoptera (bees and wasps) are concerned, Rabaud concludes as follows (p. 41): "The orientation of these insects brings into play only sensory cues. From the moment the insect starts in the direction of the nest, until that in which it arrives at the site of the nest, these cues are certainly and perhaps exclusively of a visual order.

"The manner in which these cues are registered seems complex. Besides the fact that the cues are relations between objects rather than the objects themselves, it can be stated that the flying Hymenopteron registers at departure images linked together as they would be on return, since it flies off looking at the nest. But immediately after this, it registers images of which it must on return reverse the order of connection. Experimentation proves that this latter process is a matter of no difficulty; from its first excursion abroad, the insect retraces the path it has just travelled. This result permits us also to say that the backward flight, executed by every Hymenopteron which leaves the nest for the first time has perhaps no real utility.

"As far as this is concerned, moreover, experiment furnishes reasons for thinking that it can just as well lead the insect into error, as facilitate its return. Experimenting for instance with the nest of *Vespa sylvestris*, I first of all arranged an exit by the bottom of the bell-jar; in a constant fashion the wasp which came out rose at once and flew above the bell-jar, having thus in view the upper part of the jar and its surroundings; in consequence, on returning they alighted on this part and never at the opening, which they took a certain time to find. Who, moreover, has not seen *Bombus* searching a long time in the neighbourhood of their nest before encountering it? Do not these hesitations arise precisely

* Rabaud, E., 1928. *How animals find their way about*, London, lx, 142 pp., 30 figs. Trans. I. H. Myers.

from the registration of images which do not exactly correspond with the nest site? Such hesitation is in vivid contrast with the assured flight of the Hymenopteron which follows the return path between the region in which it has been foraging and the site of the nest.

"This path doubtless improves progressively and becomes simplified; various intermediate cues fade out and disappear; it is even probable that muscular memory is substituted for visual cues over a large part of the course. In all these cases, the visual cues immediately leading to the nest persist. It is these latter of which we have been able to grasp the co-ordination into a complex of superposed or successive planes. At the nest itself olfactory, tactile, and perhaps other cues come into play.

"To sum up, in the whole course of the path analysis finds sensory cues only; at no moment does it find occasion to adopt the idea of a special sense of any kind whatsoever." (Rabaud, l.c., pp. 41–3.)

Orientation in walking insects is a much more complicated performance—so much so that more than one thoroughly reliable observer has been led to postulate a "sense of direction" beyond our ken. In the ants, much of the diversity of interpretation has been occasioned by the variation in behaviour with species. Those with well-developed eyes, for example, use visual cues—including the sun itself, and such large and distinct landmarks as hedges, walls and trees, to an extent which was not hitherto suspected. In the ants, also, the plasticity of homing behaviour reaches its climax. "Olfactory cues predominate for individuals proceeding in columns; but visual cues intervene when the trail happens to be accidentally destroyed. As for isolated ants, they follow simultaneously visual cues of various kinds—light and large objects—closely associated, and connected in addition with features of the ground, notably with the slope. Every cue is associated with all the others, but also with the topographical position of the nest, so that in the absence of any one of them, the others constitute a sufficient guide. These cues, however, are not linked in the memory of the ant in such a way that it need be obliged to pass from one to the other. For the ant, the road is not lined with a series of successive steps, so closely bound together that one evokes necessarily and exclusively the next. As in the case of the flying Hymenoptera, all takes place as if the ant registered a whole, in complete relation with the position of the nest, and registered in such a way that it is able on return to neglect zigzags and take the shortest route. In the long run, the return perhaps becomes a matter of kinæsthesis and appreciation of distance, at least from a determined point, and at a given distance from the nest.

" Without a doubt, in all cases, the ordinary sensory cues are the sole factors entering into account. The explanation of the return to the nest in no way leads us to assume the existence of any unknown sense, which would merit the name of sense of orientation. Experimentation gives evidence solely of a special process such that the insect takes the reverse, independently of visual, olfactory or tactile cues, of the direction followed on the outward journey. Certainly it indeed seems as though it actually registered a " direction ", but it registers it, according to all probability, by reference to the object on which, or before which, it finds itself. This registration, moreover, does not seem peculiar to nest-building and social insects." (Rabaud, l.c., pp. 93–4.)

NOTE 55.—The means by which bees, do, at times, communicate to their fellows in the hive the nature and whereabouts of booty, have eluded the keenest observation of bee-students up to our own day. Now, however, von Frisch has brought forward an explanation which seems to be the correct one. He published his discovery first in 1921, wrote a longer account in 1923, and a shorter one in 1924. Since his interesting observations and experiments are by no means familiar to English readers, and since they carry on very exactly the Lubbock tradition, I have thought it worth while to translate here the whole of von Frisch's 1924 acount of this important discovery.

" Hitherto the scent of flowers has been considered only an attractant for insects, facilitating their first discovery of the blossoms. This is certainly true for those bees—the so-called searchers—which go out to seek new sources of booty. In addition to this, we have in flower-scent a sign, which helps the bees—the collectors—already flying to one definite kind of flower, to recognize these flowers and to distinguish them from other blooms. Still this does not exhaust the significance of flower odour. To show clearly a third and perhaps most important rôle a fuller explanation is necessary.

"If we begin with experiment, and desire for this purpose to attract bees to the experiment-table, we first lay on it a piece of paper smeared with honey. We must often wait for hours, even for days, before a bee discovers the honey. But when one has found it, in a very short time dozens and then hundreds are on the spot, almost without exception from the same hive as the discoverer. Obviously there has been a communication of the find. How this took place was hitherto shrouded in mystery. It was, however, thought that the hive-mates noticed the rich booty of the new arrival, and followed her in the next flight to the feeding-ground.

"To throw light on the question, two conditions must be fulfilled. Firstly, a bee-hive is necessary which allows all activities inside it, on the whole of the combs, to be seen. I have on this account built observation hives in which the combs stand, instead of as otherwise behind one another, wholly beside one another, so that they form, as it were, one huge comb surface, which can be examined in its whole extent through glass panes. The animals become accustomed very quickly to the light, and do not allow their normal activities to be disturbed. Secondly, every experimental animal—and at times there are several dozens in an experiment—in the crowd of 30,000 or 50,000 bees of the colony, must be personally recognizable at the first glance. This I accomplished by a simple procedure, numbering the bees by means of indelible spots of colour. By the use of five different colours I was able to number them serially from 1–599, which was more than sufficient, and the numbers were so clear that I could read them even in flight.

"Now if we follow on her return to the observation-hive a bee which has discovered our honey-paper, or the sugar-water saucer, and filled her crop, then we observe some very extraordinary behaviour. After she has given her sweet booty to her hive-mates, which distribute the nectar more widely among the hungry sisterhood or disgorge it into the honey-cells,* she begins on the comb a kind of 'round-dance', in which she runs with quick tripping steps round and round

* Only extremely seldom do the collectors themselves empty into the honey-cells the nectar they bring in.

in a circle, then suddenly makes a sweep and revolves in the opposite direction, again swings round and describes a circle in the earlier sense, and so on. 3, 10, 20 swings may be made on the same place, and the mad dance may take a couple of seconds, half or even a whole minute.*

"Frequently it is repeated on different parts of the comb. The dance is broken off as quickly as it began, and the bee rushes hurriedly out of the flight-opening and seeks the feeding-place again.

"Since this round-dance takes place in a dense crowd of other bees, the dancer, in her circling, comes into close contact with her neighbours; these become greatly excited, turn their heads towards her, try to keep their antennæ on her abdomen and trip behind her, so that the dancing bee draws with her a tail of others, which accompany her in all the revolutions of the circular dance. Now and then one breaks out of the string, betakes herself to the flight-hole and leaves the hive. Soon afterwards the first newcomers appear at the feeding-place. They also dance when they return richly loaded, and the more numerous the dancers become, the more newcomers press on to the feeding-place. There is no doubt: the dances proclaim in the hive the news of a plentiful supply.

"But how do they communicate the whereabouts of the find? The first suggestion, that the newcomers fly direct after the dancer on her return to the feeding-place, proves to be certainly false; for in the hive some of the excited bees break off from the dancer during the dance, and others lose contact with her directly she has finished. They hasten independently of her to the flight-hole. There still remains the possibility that they lurk at the flight-hole, recognize perhaps in flight by some special sign the bees which go to rich sources of supply, and fly after them. I have therefore striven in many and time-consuming experiments, to observe these expected followers—with the final result that they were not forthcoming. Instead the dancer flies alone to the feeding-place, and, unexpected, as though called up by magic out of a trap-door, the newcomers there gather together with her.

"The problem leaves the most adventurous hypothesis inadequate. Thus I thought perhaps the dancer, through a

* In the lecture a cinematographic demonstration of the bee dance was given.

mysterious sign, communicated the bearings and the distance of the food to be found. False as the notion was, it yet assisted the inquiry. To test it, I stood a honey-saucer, on which several numbered bees were fed, 15 metres west of the observation hive. I set in the grass other honey-saucers, some at the same, others at greater or smaller distances in all directions. The surprising result was that not only that food-saucer, but all the saucers in the vicinity in a very short time were swarming with not-numbered bees (newcomers) from the observation-hive, as soon as the fed insects performed their dance in the hive. Had there been no feeding at that food-place, and thus therefore no dance in the hive, all the saucers would have remained undiscovered for hours and days.

"It follows, therefore, that the dances of the hive-mates independently of the dancer, cause an exodus and a search on every side. At once the question arises, within what radius this search takes place.

"The food-saucer of the numbered bees stayed in its place; the other honey-saucers I set in the subsequent successive experiments at increasingly greater distances from the hive, continually convinced that the distance was now too great, and continually surprised when the bees, admittedly after a longer time, but with unfailing certainty, still came. In the end the observation saucer stood in the middle of a meadow, a whole kilometre from the feeding-place and observation hive, and separated from them by hills and woods; the wait was four hours, but they came even there. As soon as the bees settled on the saucer, they were marked with paint, their departure from the saucer was signalled through a prepared line of sentries to the home hive, and a few minutes later we knew that they were not strangers from the surrounding apiaries, but insects from our observation-hive. So we may suppose that upon the dance there, first the surroundings of the hive, then gradually the more remote feeding-grounds, and finally the whole flight range are investigated.

"Thus the question of communicating the locality of the source of supply is cleared up in a manner as simple as it is satisfying. Feeding out of glass-saucers is, however, not altogether customary in bees. An experiment under somewhat more natural conditions poses at once a new problem.

"We put the glass-saucer further from the feeding place and now offer to our numbered bees in its stead, for instance, a small bunch of cyclamens, filling the bottom of the flowers with sugar-water. They forage, they dance in the hive. New bees troop out and give themselves up, on all sides, to the search. But they seek with a definite aim; for if we set a bunch of cyclamens anywhere in the vicinity, and somewhere near it in the meadow a bouquet of phlox (both without sugar-water), then the phloxes stay completely unnoticed, but dozens of bees ransack the cyclamens with an obstinacy out of all proportion to their scanty supply of nectar. But if, we take the bunch of cyclamens away from the feeding-place, and put there instead a phlox bunch supplied with sugar-water, the scene changes at the observation-place also; the interest in cyclamens flags in a short time, and in increasing numbers the newcomers turn to the phloxes and rummage in them, although their deep-seated nectar is wholly unattainable. The dancers have thus not only informed their fellows of the existence of a rich find, but have also announced the kind of flower supplying it. It is not difficult to guess that no extensive botanical bee-knowledge, no learned plant-names, but the flower scent, is the means by which this information is imparted. The odour of those flowers from which the bees have gathered the sweets still clings to their bodies when they perform their dances in the hive. The hive-mates notice the scent, and it stirs their memory * while they trip over the comb behind the dancer, whose abdomen they examine so sedulously with their olfactory organs, the antennæ. When they swarm out, they know already the smell of the blooms at which their hive-mate has profitably foraged, and they just search for this scent as they range over the neighbourhood.

"I will not tire you with a lengthy proof that here the real means of communication is the clinging flower-scent. Suffice it to remark that I have repeated with many other flowers, the experiment described above with cyclamen and phlox, constantly with positive results, even when the blooms had only a faint smell. With completely scentless flowers, however, the experiment failed. When I offered my marked bees, at the feeding-place, food from scentless, lively-coloured artificial flowers, the corresponding artificial blooms placed

* I refer to their previously mentioned excellent memory for odours.

in the surrounding meadow were not sought by the searching newcomers. If, however, I gave the artificial food flowers in question a drop of an ethereal oil—some peppermint oil—then the swarming newcomers took the liveliest interest in every object in the near and wider vicinity, whatever its shape, once it smelt of peppermint.

"Here is thus a third rôle of flower-scent, as I hinted above. The advantage to the bees, as to the plants, is obvious; for if in a given locality a new plant species comes into bloom, it suffices for one bee to discover the odorous flower, and soon its comrades stream in all directions over the fields in search of that scent. Then the first honey-flow goes to the colony of the discoverer, but the flowers have the advantage of speedy and certain pollination.

"This method of imparting information, in the simplest way, accomplishes still more. Were the collecting bees always to continue to dance, they would call ever new crowds to the blossoms they found, and finally, perhaps, more than were necessary to deal with the honey-flow. Experience shows that this does not happen, but that as a rule the number of collecting bees stands in a measurable relation to the quantity of food available. It is as though there were an understanding also on the size of the levies necessary. A further experiment supplies information: We imitate at the feeding-place a rich harvest in which we set a full saucer of sugar-water and take care that it does not become empty. The collected bees dance in the hive, draw out ever new crowds, and newcomers continually find the feeding place and swell the ranks of the foragers. Now let us imitate a scanty harvest: We replace the saucer by another containing only a piece of filter-paper moistened with sugar-water. With undiminished zeal the bees exercise their industry. But they must suck laboriously, and finally, after hard work, return with half filled honey-sacs. They dance no more, and from that moment their troops make no fresh excursion. The same applies to foraging on flowers; if these are rich in nectar, so that the collectors can quickly and easily gorge their honey-stomachs, then the bees dance in the hive and thus court new helpers. As soon as these are numerous enough to deal with the supply, the nectar of the individual flowers naturally is diminished, and only sufficient bees remain at the spot to gather the remainder.

" So it appeared that the method of announcing rich honey supplies by bees was completely cleared up—until related control experiments showed me otherwise.

" I established two feeding-places, at a similar distance from the bee-hive, but in opposite directions. At each place I numbered some bees and fed one troop plentifully from a full sugar-water saucer, the other sparingly, letting them suck blotting-paper. The richly-fed company danced on the comb, the sparsely-fed not. At both places the food was offered on an odourless substratum. The plentifully fed bees could thus in their dances communicate to their comrades no scent which would serve as an indication of their feeding-place. It was therefore anticipated that both troops would receive the same reinforcement ; for although only one company danced, still the newcomers swarming out on every side would approach both places somewhat at the same time and become attracted by the sight of the collecting bees. In actual fact, however, about ten times as many new arrivals gather with the richly-fed group as with the sparsely-fed company. It is evident that we still have one ' word ' to learn before we can understand bee-language. The well-fed bees, as they fly to the saucer and also while they sit and drink, swell out their scent-gland, a highly glandular pocket in the abdomen near the end (cf. Fig. 2),* which exhales a fruit-like odour perceptible to human olfaction. This scent, as I was able to show by special experiments, is enormously intense to the bees, and affects them at a great distance. The insects which fly to the scanty repast never once swell out the organ. It is the smell of this scent-organ which attracts the searching newcomers from a considerable radius, to the place where there is something afoot, and says to them : there is the rich bounty ! By painting over the scent-pocket with shellac, one can easily prevent the bees from evaginating the scent-organ. Then if we supply food plentifully at both stations, and varnish the scent-pockets of one group, both parties dance in the hive, but the group with the closed scent-organs receives only one-tenth as many newcomers as the other.

" If now weather conditions produce temporary exhaustion of a plentiful supply, or if, at our artificial feeding-place we

* We have not reproduced the illustrations.—Ed.

pause in our feeding, then one sees at the harvest, gleaning the remains, only single scouts from the earlier troops. If conditions alter, and the food again becomes plentiful, then as soon as the first scout with a full stomach returns home, the whole troop of its comrades, with surprising speed, cease their earlier activity. The same round-dance which the new-comers set in motion, calls the unemployed group-mates again to the field. In this also, under natural conditions, flower-scent plays an important part. If, out of the same colony, one troop of bees collect on lime-trees and another on Robinias, and the honey flow of the limes begins again after a rainy spell, the successful scouts alarm with their dances only their own group-mates, and these hasten outside to the already familiar food. The Robinia troop, however, remain entirely indifferent to the lime-scented dancers and await in stoical quietness a dancer bringing into the hive the perfume of Robinia.

" But nectar is not the only nutriment the bees need. They are well known to carry in also pollen in the form of pads, in great quantities on their hind legs. In the thoroughgoing division of labour, it is nearly always some individuals which gather nectar and others pollen. The pollen-collectors also dance, if they have found plentiful supplies. Their dance however, runs differently from the other, and from the very beginning is distinguishable from the round-dance of the nectar gatherers. Especially characteristic of it is a wagging movement of the dancer by which she formally beats her interested, closely-following hive-mates on the face and outstretched antennæ (the organs of smell) with her pollen ' leggings ', so far as she has not yet stripped these off.

" The pollen of every flower has a characteristic scent, very different from the smell of the floral leaves. And this scent of the collected pollen must far outweigh the odour of the floral leaves with which the bee has come into only transient contact. It is this which is here the means of communication.

" The proof of this statement is furnished by a simple experiment, which I will mention in conclusion.

" We form two groups of numbered pollen-collectors, of which the one gathers pollen on feeding-place A from roses, and the other at B from large bellflowers (*Campanula medium*). We now pause in the feeding, so that after a while only isolated scouts gather the residue at both places. Next we put up in place of the bellflowers, ones with their stamens removed and replaced by those of roses, the flower-base of a rose, together with the stamens springing from it, being fastened by means of an insect-pin in each bell . . . In a little while a scout of the bellflower group comes and begins without much hesitation to garner the rich supply. Thus at the bellflower feeding-place, in bellflowers, a bee of the bellflower troop collects the pollen of roses. On her return she begins to dance. She comes into lively contact with many group-mates of the bellflower troop, but not one takes any notice nor allows herself to be disturbed. The rose-collectors, however, which she approaches, rush on the dancer, trip close behind her hither and thither—soon they are outside —at the rose-place, where nothing is to be got, and where they rummage with perseverance in a couple of fallen rose-petals! The converse experiment . . . gave an entirely corresponding result. Only the scent of the pollen "leggings" could thus have deceived the bees; and since in free nature no frivolous hand exchanges the stamens, it is a trustworthy guide.

"Thus we have led the sense-physiology of bees up into the sphere of animal psychology. A sign-language has been disclosed, which in its simplicity impresses every observer. A few movements, a little scent which the bees carry into the hive from the flowers, a little fragrance which they themselves emit outside at the scene of their discovery, brings about an understanding in a way which could scarcely be better or simpler."

Since this was written, von Frisch and Roesch * have made further experiments which, in the main, confirm the previous conclusions. The newer work may be summarized as follows:

The odour of the scent-glands works specifically, in that it attracts only the bee's hive-mates and not those of a strange colony.

The round-dance of the nectar-collectors and the "wagging"-dance of the pollen-gatherers are not to be considered two different terms in "bee-language", in the

* "Neue Versuche über die Bedeutung von Duftorgan und Pollenduft für die Verständigung im Bienenvolk," *Zeits. f. wissenschfl. Biol. Abt. C, Zeits. f. vergl. Physiol.*, iv, pp. 1–21, 1926.

sense that only nectar-collectors react to the former and pollen-collectors to the latter. Under natural conditions, certainly, this is the case, but the distinguishing mark is not the form of the dance, but the scent, either of flowers or of pollen, mingled with it. The *round-dance* of a sugar-water-collector with pads of rose-pollen on its legs, or a dusting of the same on its body, alarms the rose-*pollen*-collectors.

The significance of the wagging movement so characteristic of the pollen-collector's dance lies in the dashing of the pollen pads against the olfactory organs (antennæ) of the closely-following hive-mates, and thus spreading the pollen scent through the hive to the utmost extent.

NOTE 56.—Here are inserted in the text pages 421 to 423, being Appendix H of the seventeenth edition.

NOTE 57. (See also Note 21.)

Lubbock's experiments do not prove incontrovertibly that bees can distinguish colours. It has been objected that they may distinguish only relative degrees of brightness; it has been claimed even, that they are colour-blind. We shall see how later experimenters have met these criticisms. The chief recent workers have been von Frisch, von Hess, and Lutz. The whole subject has lately been reviewed, very ably, by Munro Fox * whom we may begin by quoting :—

"Since Darwin's day it has been assumed that flying insects see the flowers by their colours and thus know which of them to visit. This satisfying assumption received a rude shock a few years ago when a German biologist named von Hess, who has studied the behaviour of all kinds of lower animals, insects and others, came to the conclusion that all of them alike are quite incapable of seeing colours. For all lower creatures the world must thus be gray. What we call colours they would see only as different monotonous shades of gray. This came of course as a bombshell to orthodox naturalists, for what then could be the *raison d'etre* of flower colours ? It would really be too self-centred to suppose that the gorgeous colours of flowers exist solely for the esthetic pleasure of men. Yet apparently he alone could appreciate these colours. Or are the colours of flowers pure accidents ? Are flowers purple or rose or blue just as an emerald is green or blood is red . . .

* 1927. Can insects see colours ? *Psyche*, London, No. 29, pp. 21–5.

"Let us look more closely into the studies of von Hess. How did he arrive at this startling conclusion that the lower creatures are colour-blind? To start with, we know that there are several sorts of colour-blind men. The most frequent variety of the disease is a condition in which persons can only see two colours, yellow and blue. What normal men call red, orange, yellow, and green, such persons call yellow in different shades. Blue-violet and purple they see as blue. Besides this fact, that only two colours are appreciated, there is another essential difference between the vision of these colour-blind people and that of normal individuals. When they look at the rainbow or spectrum, all normal people see yellow as the brightest of the colours. But colour-blind people see what we call yellowish-green—but what they call a shade of yellow—as the brightest hue. In a rarer condition of colour-blindness no colours at all are recognized. Such a completely colour-blind person sees all the colours merely as different tints of gray, some brighter, some duller. When shown the series of different colours on the spectrum, such people again choose what we call the yellowish-green as the brightest region of their grays.

"Now it is just on this distinction between the brightest region of the spectrum as appreciated by normal and by colour-blind persons that von Hess's conclusions are based.

"Many animals move toward light. This is a very well-known fact. Not only the moth flies into the flame, but numerous other lower creatures such as insects, water-fleas, worms, snails, slugs or even fishes, fly, creep or swim toward a light. Now von Hess's method of testing the colour vision of these animals was this. A dark room or aquarium containing a number of the creatures to be tested was lighted from one side. A simple lamp was not employed, but an arrangement which gave all the different spectral or rainbow colours. They chose out one particular colour and went toward it. The chosen tint was in all cases the yellowish-green. Now it is just this same tint that colour-blind people see as the brightest hue of yellow—or of gray—that they can appreciate. People with normal colour vision, however, see the pure yellow, not the yellowish-green, as the brightest colour. Therefore, von Hess concluded, the fishes, insects, and all the animals lower still on the scale of existence, are colour-blind, for they appreciate brightness just as colour-blind men do.

"But does this conclusion really follow? Do the experiments mean any more than that the brightness value for the various colours is different for the lower animals from what it is for normal man? Must we conclude that insects see no colours at all in flowers? Von Hess's conclusions have raised in the last few years a storm of protest from biologists . . .

"Verbal criticisms of von Hess's opinions, however, are insufficient. Fortunately experimental criticism is forthcoming. Most of this experimental work has been done or has been inspired by another German biologist, Professor von Frisch. He has for a number of years carried out a long and thorough investigation into the colour senses of fishes and insects."

Von Frisch's extremely interesting results we propose to give in a translation of his own words (1924, pp. 7–12).

"With the scent of honey we attract a troop of bees to a table and feed them there with odourless sugar-water out of a watch-glass. The bees suck to repletion, fly away, unload their burden in the home-hive and return immediately to the feeding-place." It is almost entirely the same bees which return again and again. "This circumstance we use to train them experimentally on one colour—perhaps blue. We set the food-glass on a blue paper and arrange around it, on the table in a chessboard pattern, gray papers of the same shape and size, but of all shades. If the training is continued for several hours or days, in which the relative position of the blue paper with the food-glass is frequently changed, we can make decisive experiments. All papers once used, and soiled with sugar-water, must be thrown away. On the table we lay a series of pure gray papers which grade in fifteen shades from white to black, but are arranged in any order in a chess-board design; and among them we introduce a blue paper, in any position save that where the last feeding took place. To exclude any odour proceeding from the individual papers we cover the whole arrangement with a sheet of glass. Over each of the sixteen papers we set a clean empty watch-glass. The bees gather at once over the blue paper and search obstinately at the empty glass for the customary food. Thus they demonstrate that they can distinguish the blue with certainty from all the shades of gray.* They therefore have a colour sense.

"Training on orange, yellow, green, violet, and purplish red succeeds as well as on blue. On the other hand bees trained on scarlet, and others fed for a long time at black paper, both apply themselves indiscriminately, to red, black and dark gray papers. Scarlet affects the bees no differently from black. Lately the same result has been obtained with other flower-visiting insects. One would not go far wrong in connecting the poverty of scarlet in our flora, long familiar to flower-biologists, but hitherto unexplained, with the red-blindness of flower-visiting insects. In other parts of the world also, red flowers among insect-pollinated plants seem to be as infrequent as with us. In sharp contrast to this stands the wide distribution of scarlet blossoms and the scarcity of blue colours among the "bird flowers" which are pollinated in America by humming-birds and in Australia by honeyeaters. The bird eye is highly receptive to red light, but strongly unreceptive, on the contrary, to blue. From this it follows that we are dealing not with an incapacity of the plant to produce this or that colour, but with an obvious adaptation to the colour sense of the flower visitors.

"Lately Kühn, partly in co-operation with the physicist Pohl,† has repeated the colour training of bees with the use of spectral light. The red-blindness of bees has been thereby confirmed: they do not perceive waves of over 65 $\mu\mu$. In other respects the training on the colours of the spectrum succeeded as certainly as that on pigment colours. In two points, however, the spectrum experiment proved superior to mine: I had obtained no training result with a certain bluish-green pigment paper, and I therefore considered the bees red-green blind. Afterwards Kühn and Pohl succeeded in training with no difficulty on a corresponding blue-green of the spectrum. They believe the bluish-green paper in

* "Fifteen shades of gray in the series are sufficient; for training on one definite shade of this gray series does not succeed in extreme cases. Moreover, in other sets of experiments I have employed considerably more finely-graded series with practically the same result."

† A. Kühn und R. Pohl, "Dressurfähigkeit der Bienen auf Spektrallinien," *Die Naturwissenschaften*, Jg., 1921, H. 37.

A. Kühn, "Versuche über das Unterscheidungsvermögen der Bienen und Fische fur Spektrallichter," *Nachr. d. Kgl. Ges. d. Wiss.*, Gottingen, Math.-physik. Klasse, 1923. [These I have not seen.—Ed.]

question to be unsaturated. Of the greatest interest, however, is the discovery—which in my experiments with pigment papers I naturally missed—that the receptivity of the bee's eye extends far into the ultraviolet, and that the ultra-violet (some 200 $\mu\mu$ to 300 $\mu\mu$) is seen as a proper colour, distinct not only from all gray shades but also qualitatively from blue. Again the question poses itself as to the connection with flower colours. Here it is not so easily answered, since our own eyes leave us in the lurch and special methods of research are required. According to a paper * just published in America, strong ultraviolet reflection by floral leaves is very widespread. A crowd of new questions arises for the flower-biologist.

"The blindness of the bee's eye to red is thus compensated by its perceptivity to ultraviolet. From another point of view, however, the colour-sense of bees falls considerably behind the performance of the human eye: it lacks all finer capacity for distinguishing shades of colour. Bees which are trained on a yellow paper go indiscriminately to orange, yellow, and grass-green papers; those accustomed to blue turn to blue, violet and purplish-red colours, in the last of which the red component, certainly, is absent for them. Kühn obtained entirely corresponding results in his spectrum-experiment: within the limits of the 650–530 $\mu\mu$, which include with us the short-waved red, yellow and green, no qualitative differences of stimulus were distinguished by the bees—nor any more within the bluish-green region of some 510–480 $\mu\mu$, which for them represents a second stimulus-quality, nor within the blue and violet region of 470–400 $\mu\mu$, nor finally within their fourth stimulus-quality of 400–300 $\mu\mu$ (ultraviolet).

"To consider the biological significance of this phenomenon in the right light, we must consider the behaviour of bees on their foraging flights. They are flower-constant insects—that is, a given individual flies, for hours or for days, only to flowers of one and the same plant species. This is advantageous to the bee, because it meets everywhere the same

* F. E. Lutz. Apparently non-selective characters and combinations of characters, including a study of ultra-violet in relation to the flower visiting habits of insects. *Ann. New York Acad. Sci.*, 29, pp. 181–283, 1924; see note 21.—Ed.

floral arrangement, with which it is familiar ; for the flowers, the constancy of the visitor is of the greatest importance for the inducing of regular cross-fertilization. Flower-constancy is, however, possible only if the bee can distinguish with certainty the favoured blossoms from the others. Now to the eye of the bee, that wealth of colour-gradations, which rejoices our own eye in a flowery meadow, is not present. So the bees can use the colours of flowers only in a limited measure, to distinguish them. They must press into service other signs. The shape of the floral leaves, the colour-patterns in multicoloured flowers, the " honey-marks " here demonstrably play a part—but they also are insufficient to explain the infallibility of foraging bees." *

Munro Fox concludes, perhaps not altogether justly in view of the red-green blindness of these insects, that " it is we who are more colour-blind, not less colour-blind than the bee ".

NOTE 58.—If blue flowers are pollinated especially by bees (see Note 57 *ante*) it occurred to me that an interesting comparison might be drawn from conditions in New Zealand, where bees are extremely poorly represented in the native insect-fauna. There are in New Zealand only twenty species of bees recorded, and these belong to the three most primitive families, with short tongues unsuitable for foraging at long-tubed flowers.† In the British Isles, which offer an area of somewhat similar size for comparison, Saunders in 1896, had already recorded 204 species of bees, including many representatives of the higher families, with long tongues ; and a considerable number has been described since.

Bees, then, are enormously more abundant in Britain than in New Zealand. What are the relative proportions of blue flowers in the two countries ? Of the New Zealand flowers, Cockayne ‡ writes : " If Nature failed to deck the forest and the grassland with beautiful blossoms, she made ample amends in the high mountains, though she was not lavish with colour, for, with a few exceptions, the flowers are white or yellow.

* Ed. note : Von Frisch then proceeds to explain the rôle of olfaction, his experiments on which have been described in Note 55 (*ante*).

† 8 *Prosopis* (Prosopidæ), 8 *Paracolletes* (Colletidæ), and 4 *Halictus* (Andrenidæ). Tillyard, *Insects of Australia and New Zealand*, Sydney, 1926, pp. 302–3.

‡ Cockayne, L, 1919, *New Zealand Plants and their Story*, pp. 100–1.

This peculiarity was first of all accounted for [by Alfred Russell Wallace] on the assumption that in New Zealand there was a great lack of insects capable of pollinating the flowers, and that bright flowers can only come into existence through their attracting insects . . ." The actual figures, compiled from Cockayne's great ecological work,* are as follows, the ferns and the wind-pollinated Gramineæ and Cyperaceæ being omitted from all the totals :

Coastal plants : 145 species, of which 60% have attractive flowers, 1 blue.

Plants of lowlands and lower hills : 342 species, of which 49% have attractive flowers, 3 blue.

Plants of the high mountains : 479 species, of which 70% have attractive flowers, 2 blue.

Thus only 1 per cent of the attractive flowers of New Zealand is blue. In Britain † there are some 1,200 species of plants with more or less attractive flowers, and the number of blue ones is 93, or nearly 8 per cent. These figures should be compared also with those of Lubbock (p. 238, quoted by Müller) for the Swiss Alps, though data for the proportion of flowers with concealed honey are not available for New Zealand.

In conclusion it may be remarked that of the few blue flowers which New Zealand does possess, there is no evidence that any are pollinated by insects. Thus the blue orchids of the genus *Thelymitra* are believed to be self-fertilized,‡ while the bright blue *Colensoa physaloides* (Campanulaceæ) is probably pollinated by birds. With regard to flowers of other colours, however, Wallace was entirely mistaken in his assumption that insects capable of flower-pollination are scarce in New Zealand. Diptera, for instance, are extremely abundant, in species and in individuals, and play an important rôle. But bees and blue flowers are certainly both very poorly represented in the Dominion, and the case may be one of indirect cause and effect.

NOTE 59.—The following is Lubbock's own note (pp. 418–19 of Appendix G in the seventeenth edition) on this passage :—

* *Die Vegetation der Erde XIV : The Vegetation of New Zealand*, 1921.

† Figures compiled from G. C. Druce, *Hayward's Botanist's Pocket Book*, 1922.

‡ Thomson, G. M., 1927, *Trans. N.Z. Inst.*, vol. lvii, p. 111.

Wasps

Mr and Mrs Peckham have published in the *Proceedings of the Natural History Society of Wisconsin* * a very interesting paper on the special senses of wasps, and their conclusions concur closely with mine.

It appears from their observations that some wasps stay out all night and return early in the morning, before the others begin coming out. For instance, on 18th August, the first wasps left the nest at 7.25 ; ten, however, had already returned, three of them before 5 a.m. It appears from their observations that the average time a wasp is absent from the nest, that is, the average length of each excursion, is forty-three minutes. They observe that this may appear inconsistent with my observations, when the trips were shorter and more numerous, one of my wasps having paid me 116 visits in fifteen hours and a half. But, as they justly observe, the cases are not comparable. My wasps and theirs were like Jacob and Ishmael—mine had everything ready prepared for them, theirs had to hunt for themselves.

As regards the sense of hearing, they repeated some of my experiments with the same results. They seem to consider that as regards the sense of colour their conclusions are somewhat at variance with mine.

As regards the supposed sense of direction they say † :—"Sir John Lubbock, in dealing with the sense of direction in ants, concluded, after a number of observations, that they were endowed with this sense in a high degree. Subsequently he discovered, quite accidentally, that the ants found their way by observing the direction in which the light was falling." My conclusion was, however, the result of many observations carried on under varied conditions, and I should hardly call it an accident.

They came to the conclusion, as I had done, that wasps have no sense of direction, that is to say in the form of a mysterious additional sense, but that, if they do not know where they are, they rise higher and higher into the air, circling as they do so, until they discover some high treetop or other object that had before served them as a landmark,

* April, 1887.

† *Proc. Nat. Hist. Soc. Wisconsin*, April, 1887, p. 113.

and that in this way they are able to make their way home. This entirely tallies with my own conclusion. It is interesting as showing that the vision of wasps must be good for somewhat distant objects.

They also found, as I had done, that their memory varied greatly in different individuals.

Reading-list

In compiling the following brief reading list I have had in mind readers of Lubbock in the earlier editions, who are not familiar with the works of Wheeler, Forel, and other special students of the social insects. If they proceed to these books, as listed below, they will find therein, especially in Wheeler's works, a very complete guide to the more specialized literature, to part of which I have referred already in the documentation to my annotations to Lubbock. I have omitted any reference to apiaristic works on the honey-bee, for these are legion.

I. General, and Bees and Wasps

Bouvier, E. L. 1919. *La vie psychique des insectes.* Paris, 300 pp., 16 figs.

Bouvier, E. L. 1922. *The Psychic Life of Insects.* Trans. of above by L. O. Howard. New York and London. xvi, 377 pp.

(A very useful study of the insect mind.)

Bouvier, E. L. 1926. *Le communisme chez les insectes.* Paris, 291 pp., 24 figs.

(An interesting account of social life among insects, written from a viewpoint somewhat different from that of Wheeler.)

Fabre, J. H. *Souvenirs Entomologiques.* Paris, 1924. 10 series, in 11 vols., definitive edition, containing a life of the author.

(A considerable portion has been translated and published in England and New York, under such titles as *The Hunting Wasps, More Hunting Wasps*, etc. The translations for which A. T. de Mattos was responsible are especially readable in that they have captured some of Fabre's inimitable style.)

Forel, A. 1908. *The Senses of Insects.* Translated by M. Yearsley. London, xv, 324 pp., 2 pls.

(A very sound account of insect psychology.)

Frisch, K. v. 1924. *Sinnesphysiologie und "Sprache" der Bienen.* Berlin, 27 pp., 3 figs.

(This is a convenient summary of von Frisch's longer works, and contains the gist of his experiments of the colour-sense, and method of communication of bees.)

Latter, O. H. 1913. *Bees and Wasps.* Cambridge, 140 pp., illus.

(A very cheap and good introduction.)

Ormerod, E. L. 1868. *British Social Wasps.* London, xi, 270 pp., 14 pls.

(This older work may still be obtained secondhand.)

Peckham, G. W. and E. G. 1905. *Wasps, Social and Solitary.* Westminster (London), xv, 311 pp., 53 figs.

Rau, P. and N. 1918. *Wasp Studies Afield.* Princeton Univ. Press, xv, 372 pp., 68 figs.

Saunders, E. 1896. *The Hymenoptera Aculeata of the British Islands.* London, viii, 391 pp., 54 col. pls.

(Also a cheaper edition with 2 plain pls.) (This is the authoritative work for the identification of the British species.)

Saunders, E. 1907. *Wild Bees, Wasps and Ants, and other Stinging Insects.* London, xiii, 144 pp., 28 figs., 4 col. pls.

Sladen, F. W. L. 1912. *The Humble-bee, its Life-history and how to Domesticate it, with Descriptions of all the British Species of Bombus and Psithyrus.* London, xiii, 283 pp., 6 pls., 34 figs.

(A comprehensive account of the habits and life of humble-bees, with very good illustrations of all the British species.)

Wheeler, W. M. 1919. "The Parasitic Aculeata, a Study in Evolution." *Proc. Amer. Phil. Soc.*, lviii, pp. 1–41.

(A fascinating essay on the origin of parasitic bees, wasps, and ants.)

Wheeler, W. M. 1923. *Social Life among the Insects.* London and New York, viii, 375 pp., 116 figs.

(This very readable work surveys all the phenomena of social life among insects, with special emphasis on the "fundamental rôle of nutrition in the development of the various insect societies." The documentary appendix is a useful list of literature arranged under the various groups concerned.

Wheeler, W. M. 1928. *The Social Insects : their Origin and Evolution.* London, xviii, 378 pp., 79 figs.

(This is an enlarged and revised translation of the same author's *Les sociétés d'insectes, leur origine, leur évolution*, which appeared in Paris in 1926. It attempts to answer the questions : (1) "What are the social insects ? (2) "Can they be shown to have had an evolution ? " (3) "If so, what are the peculiarities of this evolution, and to what methods must we resort for their elucidation ? " and (4) "To what general causes or conditions may we assign this evolution ? " In addition to the specific problems of the evolution of the various social insects, the book deals with polymorphism, the "reciprocal activities or intercommunication of stimuli and food (trophallaxis) ", and "the various types of parasitism that have developed out of this reciprocity, both among the social insects themselves and between them and alien insects ". The final chapter discusses "the probable course of future development in insects societies or their fate on a planet, the natural balance of whose faunas and floras is being rapidly disturbed by a much younger and more powerful social animal—man ".

The bibliography will be found especially valuable to recent literature not only on social insects in particular, but also on social animals in general, and on the numerous philosophical questions raised in the text.)

II. Ants

Bailey, I. W. 1922. "The Anatomy of Certain Plants from the Belgian Congo, with special reference to Myrmecophytism." Pp. 585–621, pls. 30–45, in Wheeler's work (1922) cited below.

(A valuable account of the anatomy of a number of "ant-plants " with a discussion of the various theories from the plant morphologist's point of view.)

Bequaert, J. 1922. "The Predaceous enemies of Ants." Pp. 271–332 and pls. 24, 25, in Wheeler's work (1922) cited below.

(A very thorough summary of our present knowledge, with some extremely interesting data on the giant scaly ant-eaters of Central Africa.)

Bequaert, J. 1922. "Ants in their Diverse Relations to the Plant World." Pp. 333–583, pls. 26–9, and figs. 77–100, in Wheeler's work (1922) cited below.

(A very authoritative contribution to this controversial subject, by one whose botanical training, entomological attainments, and wide field experience render his views peculiarly valuable. A bibliography of 53 pages surveys the extensive literature very adequately.)

Dodd, F. P. 1912. Some remarkable ant-friend Lepidoptera of Queensland. *Trans. Ent. Soc. London,* pp. 577–90, 1 pl.

(One of the weirdest stories in the annals of entomology.)

Donisthorpe, H. St. J. K. 1927a. *British Ants: their Life-history and Classification.* London, second edition, revised and enlarged, xvi, 436 pp., 18 plates, 93 diagrams.

(A clear, comprehensive, and indispensable guide to the study of British ants from every point of view. It contains an excellent bibliography of the English literature.)

Donisthorpe, H. St. J. K. 1927b. *The Guests of British Ants: Their Habits and Life-histories.* London, xxiii, 244 pp., 16 pls., 55 figs.

(An admirable companion volume to the above. It is especially rich, like the other, in local records.)

Forel, A. 1928. *The Social World of Ants Compared with that of Man.* Trans. C. K. Ogden. London and New York. 2 vols., xiv, 551 and xx, 445 pp., 24 pls., 138 figs.

(An immense but eminently readable work, containing a mass of details on every aspect of the life of ants. It represents the last great contribution of one of the greatest of myrmecologists, and embodies an attempt to bring together all the strings of his life-work. It is well-illustrated by useful figures and extremely beautiful plates. No other work contains so much data, and it will probably be the last attempt to condense all the phenomena of ant-life in a single book.)

Réaumur, R. A. F. de. 1926. *The Natural History of Ants.* From an unpublished manuscript in the Archives of the Academy of Sciences of Paris. Translated and annotated by William Morton Wheeler. New York, xvii, 280 pp., 4 pls.

(The manuscript of Réaumur, the first great experimental entomologist, is printed as it stands, and is followed by a very able translation with annotations by Professor Wheeler, forming an intensely interesting volume.)

Sernander, R. 1906. "Entwurf einer Monographie der europäischen Myrmecochoren." *Kungl. Svenska Vetensk. Akad. Handl.,* xli, pp. 1–410, 11 plates, 29 text-figs.

(This is a tremendously detailed work dealing with the activities of European ants in carrying seeds.)

Wasmann, E. 1920. *Die Gastpflege der Ameisen, ihre biologischen und philosophischen Probleme.* Schaxel's Abhandl. Theoret. Biol., Heft 4, xvii, 176 pp., 2 pls.

(An important summary of the relations between the ants and their guests, by the foremost living student of myrmecophily.)

Wasmann, E. 1923. Die Larvenernährung bei den Ameisen und die Theorie der Trophallaxis. *Mem. Pontif. Accad. Romana*, (2), vi, pp. 67–87, 1 fig.

(Chiefly important as a criticism of Wheeler's theory of trophallaxis (1918).)

Wasmann, E. 1925. *Die Ameisenmimikry. Ein exakter Beitrag zum Mimikryproblem und zur Theorie der Anpassung.* Schaxel's Abhandl. Theoret. Biol., Heft 19, xii, 164 pp., 3 pls.

(Wasmann considers that true ant-mimicry exists only among the guests of ants. This phenomenon he considers in great detail here, with special reference to "touch-mimicry".)

Wheeler, W. M. 1910. *Ants, their Structure, Development, and Behaviour.* New York, xxv, 663 pp., 286 figs.

(This will long remain the standard book on ants, and is in many respects a model for any comprehensive work on a single group of insects. The copious bibliography of seventy pages serves as a guide to all the more important literature up to within a year or so of 1910.)

Wheeler, W. M. 1918. A study of some ant-larvæ, with a consideration of the origin and meaning of the social habit among insects. *Proc. Amer. Philos. Soc.*, lvii, pp. 293–343, 12 figs.

(A very important paper, introducing the theory of "trophallaxis", as the foundation of the social habit in insects.)

Wheeler, W. M. 1922. Ants of the American Museum Congo Expedition. A contribution to the myrmecology of Africa, with the collaboration of J. Bequaert, I. W. Bailey, F. Santschi, and W. M. Mann. *Bull. Amer. Mus. Nat. Hist.*, vol. 45, 1139 pp., 45 pls., 47 maps, 103 figs.

(A monumental work containing far more than an account of African ants. An especially useful feature is a complete key to the genera of ants for the world. For other contributions of general interest see under Bequaert and Bailey.)

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Belt, T. *The Naturalist in Nicaragua.*

Bert, Paul. "Les animaux voient-ils les mêmes rayons lumineux que nous ?" *Arch. de Physiol.*, 1869.

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Boissier de Sauvages, l'Abbé. "L'origine du Miel." *Journ. de Physique*, vol. i.

Büchner, L. *Mind in Animals.*

Buckley, S. B. "On Myrmica molefaciens." *Proc. Acad. Nat. Sci. Philadelphia*, 1860.

Burmeister, H. *Manual of Entomology.*

Curtis, J. "On the Genus Myrmica." *Trans. Linn. Soc.*, 1854.

Darwin, C. *Origin of Species.*

Delpino, F. *Sui rapporti delle Formiche colle Tettigometre.*

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Dujardin, F. "Obs. sur les Abeilles." *Ann. des Sci. Nat.*, 1852.

Edwards, H. "Notes on the Honey-making Ants." *Proc. California Acad.*, 1873.

Elditt, H. L. *Die Ameisen-Colonien u. deren Mitbewohner.*

Emery, C. *Saggio di un ordinamento naturale dei Mir micidei.*

Emery, C. "Le Formiche ipogei." *Ann. Mus. Civ. di St. Nat. di Genova.*

Forel, A. *Fourmis de la Suisse.*

Gélieu, J. de. *Le Conservateur des Abeilles.*

Gould, Rev. W. *Account of English Ants.*

Gräber, Vitus. *Die Tympanalen-Sinnesapparate der Orthopteren.*

Gredler, V. *Der zoologische Garten.*

Grimm. "Die Myrmecophilen." *Stettin. Ent. Zeits.*, 1845.

Hagens, Herr von. "Ueber Ameisengäste." *Berlin. Ent. Zeits.*, 1865.

Hagens, Herr von. "Ueber Ameisen mit gemischten Colonien." *Berlin. Ent. Zeits.*, 1867.

Heer, O. "Die Hausameisen Madeiras." *Zürich. Nat. Ges.*, 1852.

Huber, P. *Natural History of Ants.*

Huxley, T. H. "On the Reproduction of Aphis." *Trans. Linn. Soc.*, xxii, 1859.

Kerner, Dr A. *Flowers and their Unbidden Guests.* Trans. by Ogle.

Kirby and Spence. *Introd. to Entomology.*

Landois, Dr H. *Thierstimmen ;* also *Zeits. für Wiss. Zool.*, 1867.

Langstroth, L. L. *Treatise on the Honey Bee.*

Latreille, P. *Hist. Nat. des Fourmis.*

Lespès, C. "Sur les Mœurs de Lomechusa paradoxa." *Ann. des Sci. Nat.*, 1863.

Lincecum, Gideon. "On the Agricultural Ant of Texas." *Linn. Journal*, 1861.

LONG, Col. C. G. *Central Africa.*
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LUBBOCK, Sir J. "On Some Points in the Anatomy of Ants." *Micros. Soc.*, 1877.
LUND, M. "Lettres sur les Habitudes de quelques Fourmis du Brésil." *Ann. des Sci. Nat.*, xxiii, 1831.
McCOOK, H. C. "Note on Adoption of a Queen Ant." *Proc. Acad. Nat. Sci. Philadelphia*, 1879.
McCOOK, H. C. *On the Nat. Hist. of the Agricultural Ant of Texas.*
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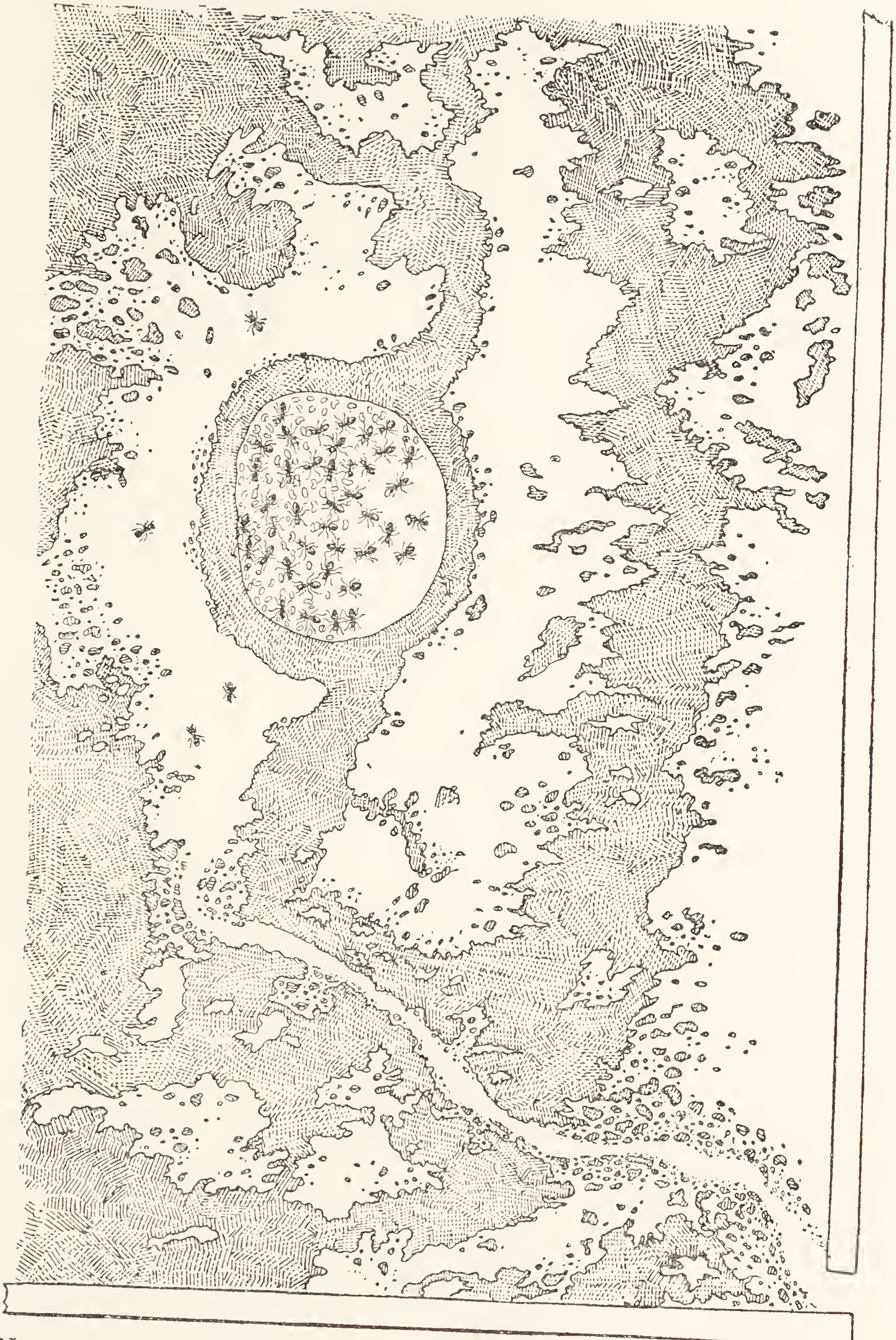
PLATE V.



NEST OF *TETRAMORIUM*.

Part of one of my Ant cases, showing circular nest, with pathway leading to the opening. The Ants enter the circular fortification by one or two tunnels not visible in the figure.

NEST OF

Showing the entrance, vestibule, main chamber with pillars, and inne
larvæ, sorted according to ages; and two kinds of domestic animals
The shaded part represents earth. See p. 32. This is the

US NIGER

; the queen surrounded by workers; a group of pupæ, and several of
small Beckias and the blind Woodlice (*Platyarthrus Hoffmanseggii*).
nest as that represented on p. 33, but seven years afterwards.

[*End of Book*